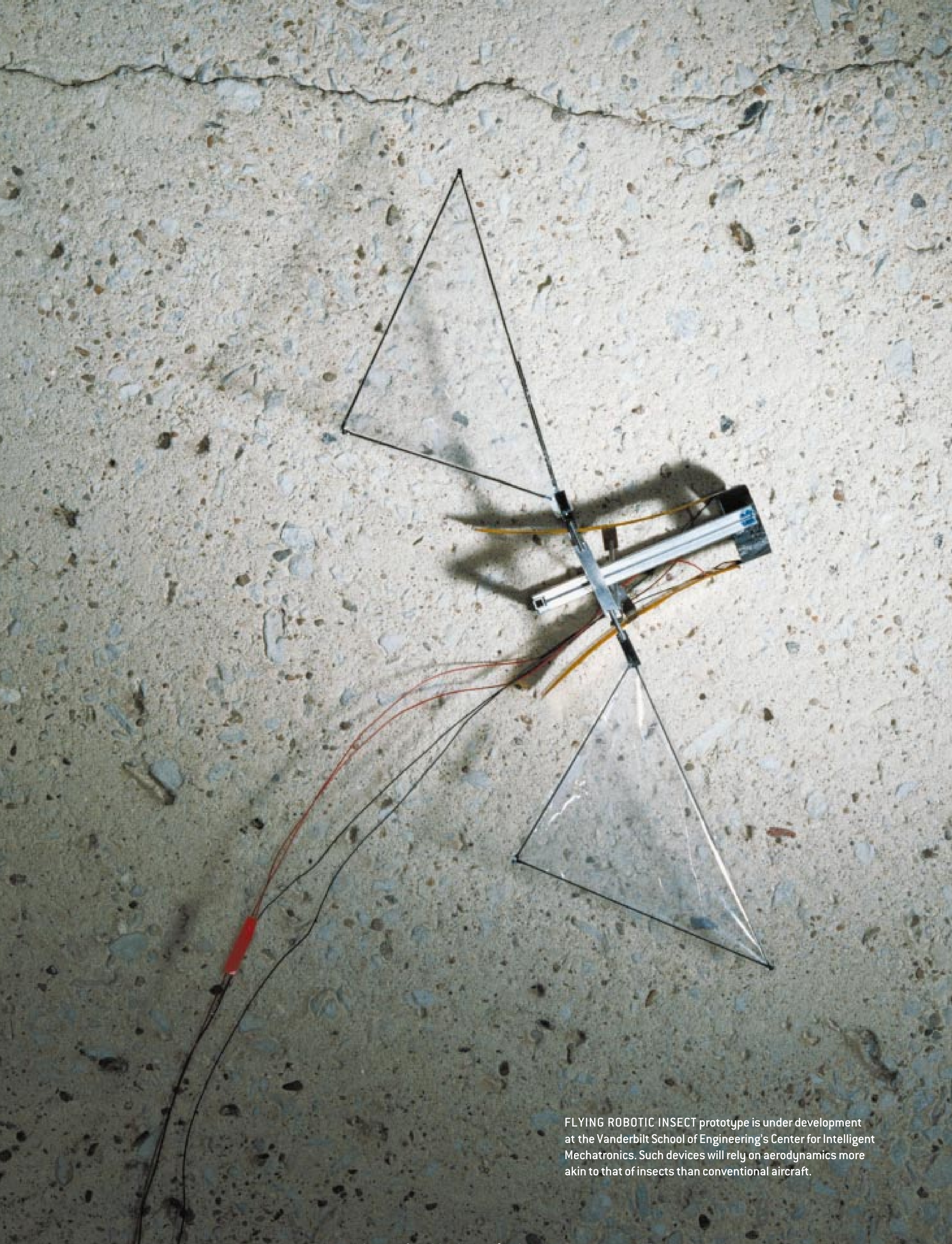


FLYING ROBOTIC INSECT prototype is under development at the Vanderbilt School of Engineering's Center for Intelligent Mechatronics. Such devices will rely on aerodynamics more akin to that of insects than conventional aircraft.

Solving the Mystery of INSECT FLIGHT

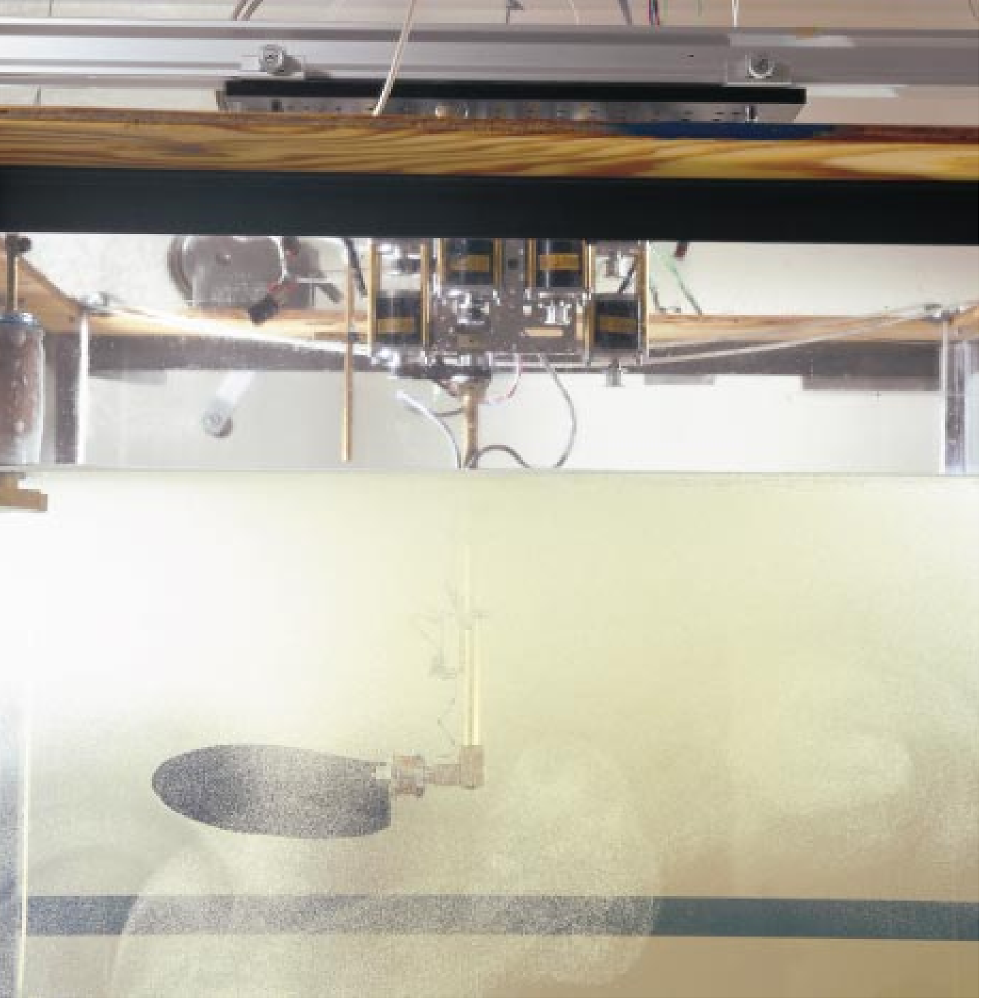
INSECTS USE A COMBINATION OF AERODYNAMIC EFFECTS TO REMAIN ALOFT

BY MICHAEL DICKINSON

Photographs by Timothy Archibald

In a two-ton tank of mineral oil, a pair of mechanical wings flap continuously back and forth, taking a leisurely five seconds to complete each cycle. Driven by six computer-controlled motors, they set the fluid swirling, a motion that is revealed by millions of air bubbles immersed in the liquid (the tank has a strong resemblance to a giant glass of beer, albeit one with a 60-centimeter-wingspan mechanical fly thrashing around in it). Flashing sheets of green laser light illuminate the scene, and specialized video cameras record the paths of the glistening, churning bubbles. Sensors in the wings record the forces of the fluid acting on them at each moment.

My research group constructed this odd assortment of specialized equipment to help explain the physics of one of the commonest of occurrences—the hovering of a tiny fruit fly. The fly knows nothing of the aerodynamics of vortex production, delayed stall, rotational circulation and wake capture; it merely employs their practical consequences 200 times each second as its wings flap back and forth. The fly's mechanical simulacra, dubbed Robofly, imitates the insect's flapping motion, but at a thousandth the speed and on a 100-fold larger scale. Awed by the rapidity and the small size of the real thing, my colleagues and I pin our hopes on Robofly for understanding the intricate aerodynamics that allows insects to do what they do so routinely—that is, how they are able to fly.



ROBOFLY FLAPPING SLOWLY in viscous mineral oil simulates the aerodynamics of fruit-fly wings flapping rapidly in air. Laser beams illuminate air bubbles in the oil to reveal the intricate flows produced, and sensors in the wings record the forces generated.

As measured by sheer number of species, ecological impact or total biomass, insects are the dominant animals on our planet. Although numerous factors contribute to their extraordinary success, the ability to fly ranks high on the list. Flight enables insects to disperse from their birthplace, search for food over large distances and migrate to warmer climes with the changing seasons. But flight is not simply a means of transport—many insects use aerial acrobatics to capture prey, defend territories or acquire mates. Selection for ever more elaborate and efficient flight behavior has pushed the design of these organisms to the limit. Within insects we find the most sensitive noses, the fastest visual systems and the most powerful muscles—all specializations that are linked one way or another to flight behavior. Until recently, however, an embarrassing gap has marred our understanding of insect flight: scientists have had a difficult time explaining the aerodynamics of how insects generate the forces needed to stay aloft.

That difficulty has even made its way into an urban legend of science, typically recounted as "a scientist 'proved' that a bumblebee can't fly" and often cited as an inspiring example for persevering in the face of overbearing dogma. The bumblebee story can be traced back to a 1934 book by entomologist Antoine Magnan, who refers to a calculation by his assistant André Sainte-Laguë, who was an engineer. The conclusion was presumably based on the fact that the maximum possible lift produced by aircraft wings as small as a bumblebee's wings and traveling as slowly as a bee in flight would be much less than the weight of a bee.

In the decades since 1934, engineers and mathematicians have amassed a body of aerodynamic theory sufficient to design Boeing 747s and stealth fighters. As sophisticated as these aircraft may be, their design and function are based on steady-state principles: the flow of air around the wings and the resulting forces generated by that flow are stable over time. The reason insects represent such a challenge is that they flap and rotate their wings from 20 to 600 times a second. The resulting pattern of airflow creates aerodynamic forces that change continually and confound both mathematical and experimental analyses.

In addition to resolving an old scientific puzzle, understanding how insects fly may have practical applications. Recently engineers have begun to explore the possibility of developing thumb-size flying robots for applications such as search and rescue, environmental monitoring, surveillance, mine detection and planetary exploration. Although humans have succeeded in constructing model aircraft as small as a bird, no one has built a fly-size airplane that can fly. The viscosity of air has greater importance at such tiny sizes, damping out the kind of airflows that keep larger aircraft aloft. Insects flap their wings not simply because animals have never evolved wheels, gears and turbines, but because their Lilliputian dimensions require the use of different aerodynamic mechanisms. Robotic insects of the future may owe their aerodynamic agility to their natural-world analogues.

A BLUR OF WINGS

IT IS APPARENT to the casual observer that a hovering insect, its wings a blur, does not fly like an aircraft. Much less obvious is the complexity of the flapping motion. Insect wings do not merely oscillate up and down like paddles on simple hinges. Instead the tip of each wing traces a narrow oval tilted at a steep angle. In addition, the wings change orientation during each flap: the topside faces up during the downstroke, but then the wing rotates on its axis so that the underside faces up during the upstroke.

THE AUTHOR

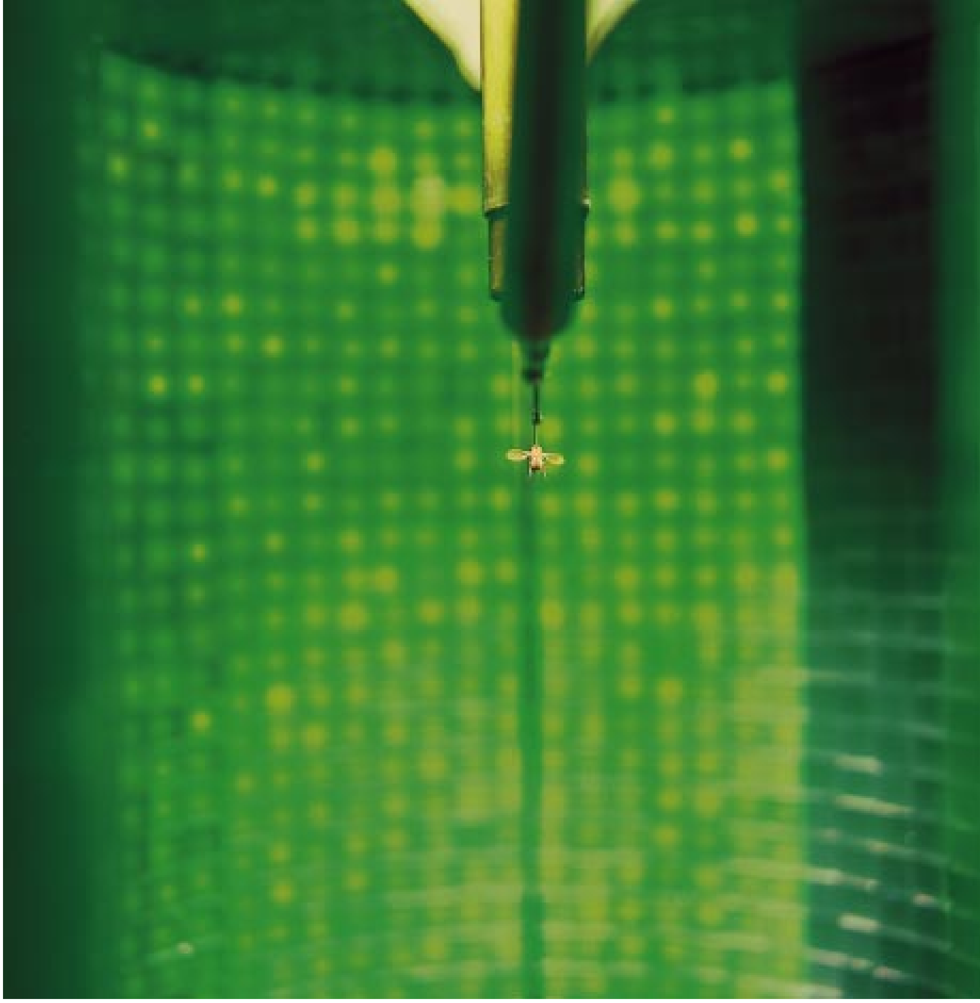
MICHAEL DICKINSON began his career as a neurobiologist, focusing on the cellular basis of behavior. His interest in flight developed from an investigation of tiny sensory structures that sense the bending of a wing as it flaps. He now attempts to study behavior in a more integrated fashion, by synthesizing the tools and analyses of biology, physics and engineering. He is a professor in the department of integrative biology at the University of California, Berkeley.

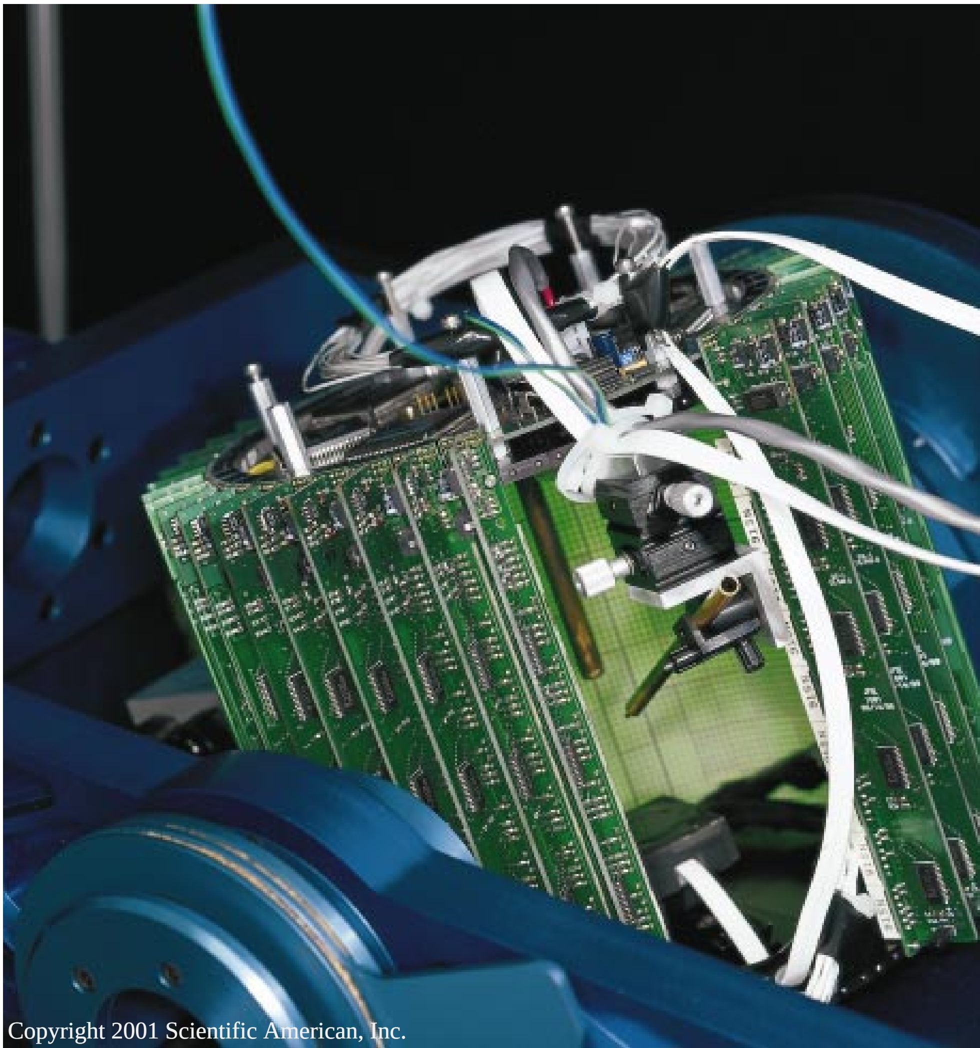
The earliest analyses of insect flight tried to apply conventional steady-state aerodynamics, the approach that works for aircraft wings, to these complex motions. Such attempts are not as naive as the infamous bumblebee computation, because they take into account the changing velocity of the wings as they flap through the air. Imagine freezing the insect's wing at one position in the stroke cycle and then testing it in a wind tunnel with the wind velocity and the wing orientation set to mimic the precise movement of the wing through the air at that instant. In this way, one could measure the aerodynamic force acting on the wing at each moment.

If this steady-state theory were sufficient, the average force, computed by adding up the forces for all the different wing positions throughout the stroke, should point upward and equal the insect's weight. Even in the late 1970s experts disagreed about whether such analysis could explain how insects stay aloft. In the early 1980s Charles Ellington of the University of Cambridge carefully reviewed all available evidence and concluded that the steady-state approach could not account for the forces required. The search for dynamic, "unsteady flow" mechanisms that could explain the enhanced performance of flapping wings took off with renewed vigor.

The distribution of velocities and pressures within a fluid is governed by the Navier-Stokes equations, which were formulated in the early 1800s. (For the purpose of analyzing aerodynamics, air is simply a very low density fluid.) If we could solve these equations for a flapping insect wing, we could fully characterize the aerodynamics of the insect's flight. Unfortunately, the complex motion of the wing renders this problem excruciatingly hard to simulate with even the most powerful computers.

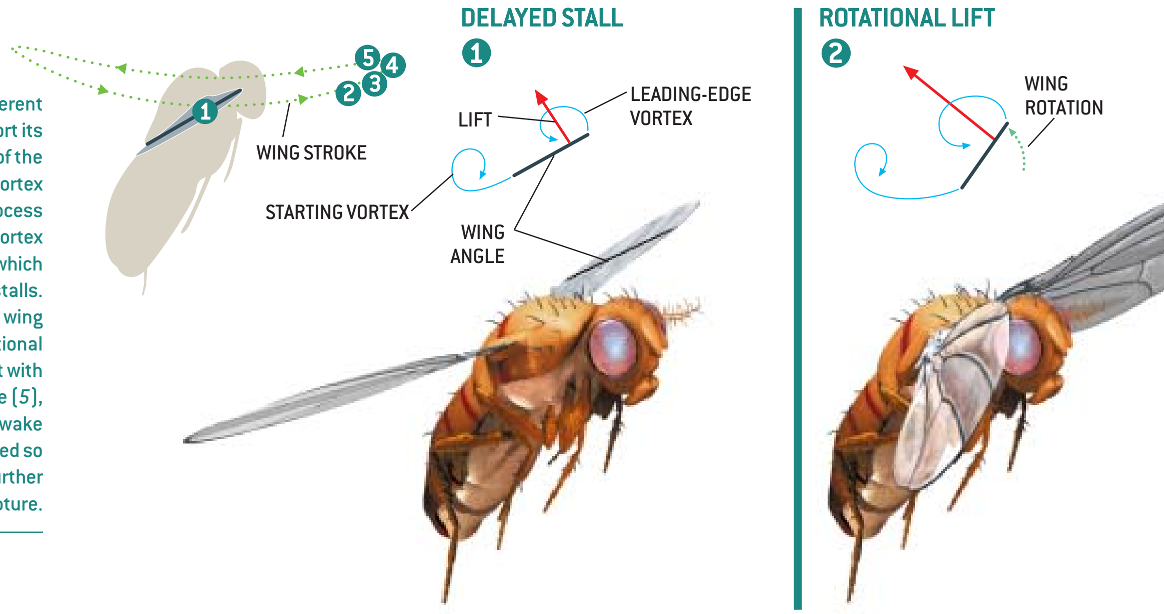
If we can't solve the problem by pure

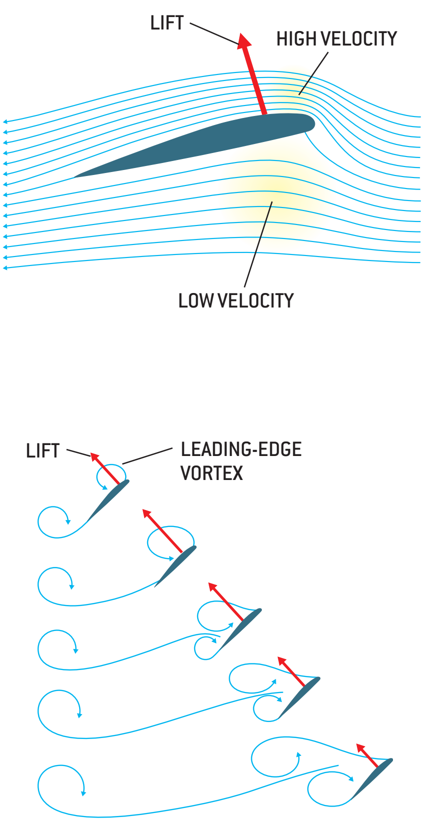




TETHERED FLY is seen against the backdrop of a virtual-reality arena (*top*). A computer controls the thousands of green diodes to produce the illusion (for the fly) of objects moving according to the fly's aerodynamic maneuvers. A similar arena is mounted on a gimble (*bottom*) to simulate the turns, rolls and yaws of free flight.

FRUIT FLY USES three different aerodynamic mechanisms to support its weight in the air. During much of the wing stroke (*1*), a leading-edge vortex forms and increases lift, a process called delayed stall because the vortex does not have time to detach, which is what happens when an aircraft stalls. At the end of a stroke (*2, 3, 4*), the wing rotates, which produces rotational lift analogous to a tennis ball hit with backspin. At the start of the upstroke (*5*), the wing passes back through the wake of the downstroke. The wing is oriented so that this increased airflow adds further lift, a process called wake capture.





AIRCRAFT WING generates lift by steady-flow aerodynamics (*top*). Smooth flow over the top of the wing is faster than that under the wing, producing a region of low pressure and an upward force. If the angle of attack is too great (*bottom*), the wing stalls. When a stall begins, a leading-edge vortex forms with a high flow velocity that momentarily increases lift. The vortex quickly detaches from the wing, however, greatly reducing lift.

theory and computation, can we instead directly measure the forces generated by a flapping insect wing? Several groups have made informative and valiant efforts and are developing imaginative new approaches, but the delicate size and high speed of insect wings make force measurements difficult.

To circumvent these limitations, biologists studying animal locomotion frequently employ scale models—the same trick used by engineers to design planes, boats and automobiles. Engineers scale their vehicles down in size, whereas insect-flight researchers enlarge and slow the wings to a more manageable size and speed. Such models produce meaningful aerodynamic results provided they meet a key condition regarding the two forces that an object encounters within a fluid: a pressure force produced by fluid inertia and a shear force caused by fluid viscosity. The inertial force is essentially that needed to push along a mass of fluid and is larger for denser fluids. Viscosity is more like friction; produced when adjacent regions of fluid move at different velocities, it is what makes molasses hard to stir. The underlying physics of the real and the model animals is identical as long as both have the same ratio of inertial to viscous forces, called the Reynolds number.

The Reynolds number increases in proportion to an object's length and velocity and the density of the fluid; it decreases in proportion to the fluid's viscosity. Being large and fast, aircraft operate at Reynolds numbers of about a million to 100 million. Being small and slow, insects operate at Reynolds numbers of around 100 to 1,000 and under 100 for the tiniest insects, such as thrips, which are a common garden pest.

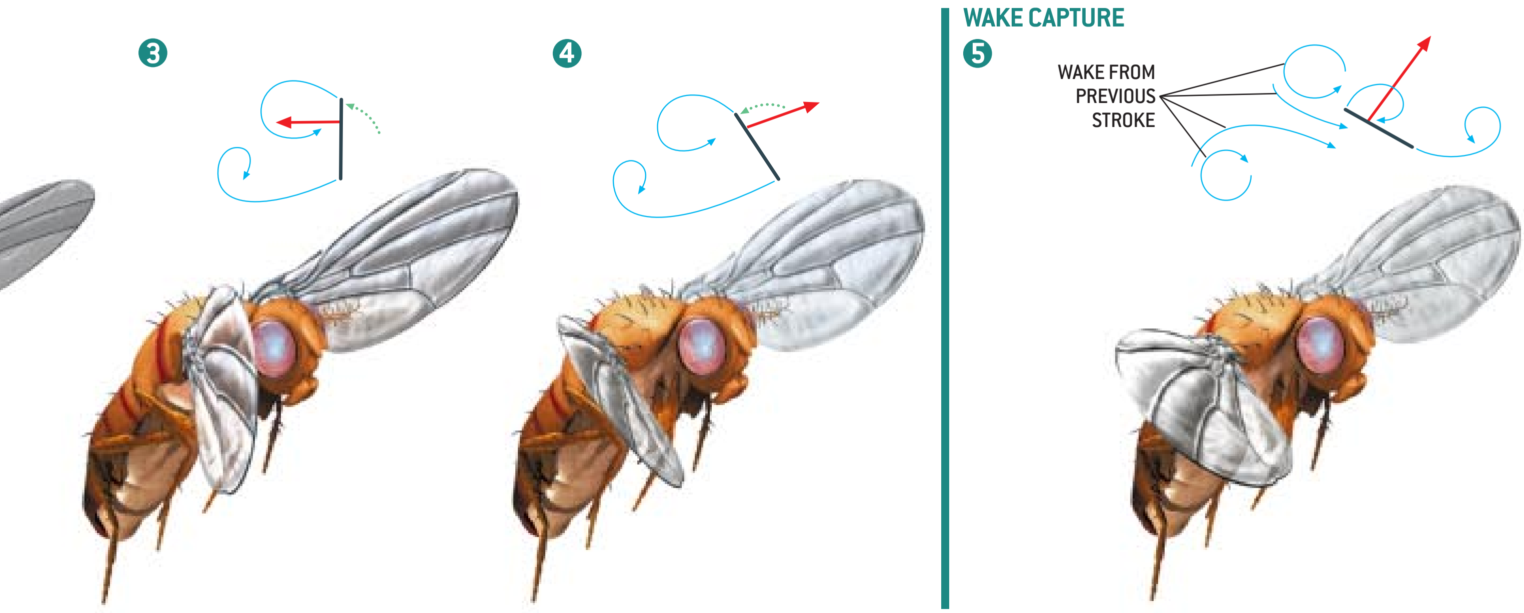
DELAYED STALL

TO GAIN SOME INSIGHT into how a flapping fruit-fly wing generates aerodynamic force, in 1992 Karl Götz and I, both then at the Max Planck Institute for Biological Cybernetics in Tübingen, Germany, built a model wing consisting of a five-by-20-centimeter paddle connected to a series of motors that moved it within a large tank of thick sugar syrup. That combination of increased size and viscosity, and the slower flapping rate, resulted in the same Reynolds number, and thus the same physics, as a fruit-fly wing that is flapping in air.

We equipped the wing with a force sensor to measure the lift and drag generated as it moved through the sticky fluid. We put baffles at the ends of the wing to inhibit flow along the length and around the edge of the wing. Simple aerodynamic models often use this technique: it effectively reduces the flow from three dimensions to two, which makes the analysis easier but at the risk of missing important effects.

Our experiments with this model wing and work in other laboratories helped to uncover one possible solution to the conundrum of insect flight: de-

ILLUSTRATIONS BY BRYAN CHRISTIE

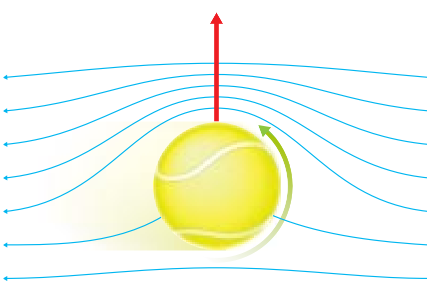


layed stall. In an aircraft, stall occurs if the angle that the wing cuts through the air—the angle of attack—is too steep. At shallow angles of attack, the air splits at the front of the wing and flows smoothly in two streams along the upper and lower surfaces. The upper flow travels faster, resulting in a lower pressure above the wing, which sucks the wing upward, producing lift. When the angle of attack is too steep, however, the upper flow cannot follow the contour of the upper surface and separates from the wing, resulting in a catastrophic loss of lift.

How can stall, which is disastrous for an airplane, help to lift an insect? The answer lies in the rate at which the wings flap. Wings do not stall instantly; it takes some time for the lift-generating flow to break down after the angle of attack increases. The initial stage of stall actually briefly increases the lift because of a short-lived flow structure called a leading-edge vortex. A vortex is a rotating flow of fluid, as occurs in tornadoes or the little whirlpool in a draining bathtub.

The leading-edge vortex forms just above and behind the wing's leading edge, like a long cylindrical whirlpool turned on its side. The airflow in the vortex is very fast, and the resulting very low pressure adds substantial lift. This effect was first recognized by aeronautics engineers in England in the early 1930s, but it is too brief to be of use to most aircraft. Very quickly, the vortex detaches from the wing and is shed into the aircraft's wake, and lift drops precipitously, as does the plane. The wing strokes of insects, however, are so brief that the wing flips over and reverses direction, producing a new vortex in the opposite direction immediately after the previous one is shed.

These results, obtained with simplified two-dimensional models, were extended to three dimensions in the mid-1990s by Ellington and his co-workers at Cambridge. His group studied the large hawkmoth, *Manduca sexta,* flying tethered in a wind tunnel, as well as a fully three-dimensional robotic moth. Lines of smoke (called a smoke rake) revealed that a vortex is indeed attached to the wings' leading edges during the downstroke. Ellington's team suggested that an axial flow of air from base to tip of the wings enhanced the effect by reducing the strength of the vortex but increasing its stability and allowing it to remain attached to the wings throughout the stroke. Such axial

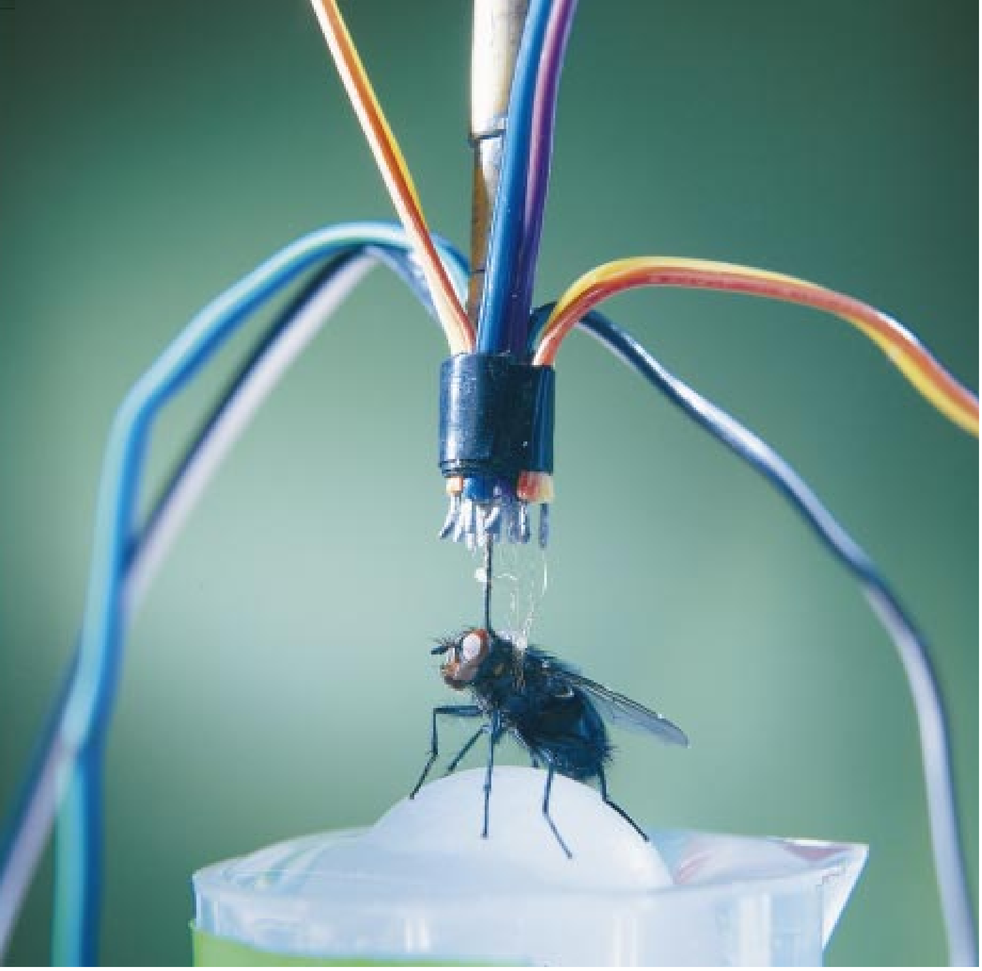


AIRFLOW AROUND a tennis ball that is hit with backspin generates rotational lift. Insects use the same phenomenon by rotating their wings at the end of each stroke.

The first animals to evolve active flight were insects.

Most insects have two pairs of wings. The hind wings of flies, however, have evolved into tiny sensory organs that function as gyroscopes, monitoring the orientation of the fly's body.

Per second, flying expends about 10 times more energy than locomotion on the ground. On the other hand, per kilometer traveled, flying is four times more energy-efficient than ground locomotion. Thus, flying is very hard to achieve but has great value for organisms that can do it.



BLOWFLY IS WIRED for studies that relate the electrical activity in steering muscles to changes in wing motion that occur during steering maneuvers.

Insects possess the most diverse wing structure and kinematics of all flying animals.

Flight muscle of insects exhibits the highest-known metabolic rate of any tissue.

Air is more kinematically viscous than water: its ratio of viscosity to density is higher. That ratio is what matters for fluid dynamics.

flow might be especially important for large insects such as hawkmoths and dragonflies that flap their wings over a great distance during each stroke.

Although identifying this effect solved a major piece of the puzzle, various lines of evidence suggested that insects harnessed other mechanisms in addition to delayed stall. First, the extra force produced by delayed stall is enough to explain how an insect remains airborne but insufficient to explain how many insects can lift almost twice their body weight. Second, several investigators have attempted to measure the forces an insect creates by tethering it to a sensitive force transducer. Such experiments must be viewed cautiously, because tethered animals may not behave identically to freely flying animals, but the precise timing of the forces is not easily explained by delayed stall. For example, when Götz used a laser diffraction technique to measure the forces generated by a fruit fly, he found that the greatest forces occurred during the upstroke—at a time when the forces resulting from delayed stall are expected to be weak.

To search for additional unsteady mechanisms, in 1998 Fritz-Olaf Lehmann, Sanjay P. Sane and I constructed a large model of a flapping fruit fly, *Drosophila melanogaster*—the Robofly described earlier. The viscous mineral oil within the tank makes the 25-centimeter robot wings flapping once every five seconds dynamically similar to 2.5-millimeter fruit-fly wings flapping 200 times a second in air. We measured two critical properties—the aerodynamic forces on the wings and the fluid flow around them—that are nearly impossible to determine on real fly wings. Although Robofly is designed to mimic a fruit fly, by programming the six motors that drive the two wings, we can re-create the wing motion of numerous insect species. In addition, we can make Robofly flap its wings in any way required to test specific hypotheses—a luxury not afforded by real animals, which tend to get temperamental under laboratory conditions.

ROBOFLY'S RESULTS

WHEN ROBOFLY FLAPPED like a fruit fly, we measured a curious pattern of forces. The wings generated momentary strong forces at the beginning and end of each stroke that could not be easily explained by delayed stall. These force peaks occurred during stroke reversal, when the wing slows down and rapidly rotates, suggesting that the rotation itself might be responsible.

Rotating objects moving through the air produce flows similar to those that lift a conventional wing. A tennis ball hit with backspin pulls air faster over the top, causing the ball to rise. Conversely, topspin pulls air faster underneath, pushing the ball down. A flat wing is different from a spherical ball, but rotation of a wing should produce some lift by the same general mechanism.

We tested our hypothesis by modifying the precise moment in the stroke cycle when the wing flips. If a wing rotates at the end of one stroke, as in a normal fly stroke, the wing's leading edge rotates backward relative to the direction in

PROTOTYPE MICROMECHANICAL flying insect is being developed by the Robotics and Intelligent Machines Laboratory at the University of California at Berkeley. The design parameters are based on the blowfly *Calliphora*.

which the wing is moving and the wing should develop some upward force—analogous to a tennis ball hit with backspin. If the wing rotates late, at the beginning of the next stroke, the leading edge moves forward relative to the direction of motion, and the wing will develop a downward force analogous to topspin. Robofly's data were in complete agreement with these expectations, indicating that flapping wings develop significant lift by rotational circulation.

There remained, however, another significant force peak in Robofly's data, occurring at the start of each downstroke and upstroke, that rotational circulation could not easily explain. Several sets of experiments indicated that this peak was caused by a phenomenon called wake capture—the collision of the wing with the swirling wake of the previous stroke.

Each stroke of the wing leaves behind a complicated wake consisting of the vorticity it produced by traveling and rotating through the fluid. When the wing reverses direction, it passes back through this churning air. A wake contains energy lost from the insect to the fluid, so wake capture provides a way for the insect to recover some of that energy—to recycle it, one might say. We tested the wake-capture hypothesis by bringing Robofly's wings to a complete stop after flapping back and forth. The stationary wings continued to generate force because the fluid around them was still moving.

Although wake capture must always occur at the start of each stroke, as with rotational circulation the fly can manipulate the size and direction of the force produced by changing the timing of wing rotation. If the wing rotates early, it already has a favorable angle of attack when it collides with the wake, producing a strong upward force. If the wing rotates late, collision with the wake generates a downward force.

Together wake capture and rotational circulation also help to explain the aerodynamics of flight control—how flies steer. Flies are observed to adjust the timing of wing rotation when they turn. In some maneuvers, the wing on the outside of a turn rotates early, producing more lift, and the wing on the inside of a turn rotates late, generating less lift; the net force tilts and turns the fly in the desired direction. The fly has at its disposal an array of sophisticated sensors, including eyes, tiny hind wings that are used as gyroscopes, and a battery of mechanosensory structures on the wings that it can use to precisely tune rotational timing, stroke amplitude and other aspects of wing motion.

BRIDE OF ROBOFLY

THE WORK of numerous researchers is beginning to coalesce into a coherent theory of insect flight, but many questions remain. Insects have a vast array of body forms, sizes and behaviors, ranging from tiny thrips to large hawkmoths; from two-winged flies such as fruit flies to lacewings that flap two pairs of wings slightly out of sync and tiger beetles that have two large stationary wings (their elytra, which form their carapace when on the ground) in addition to the two wings that flap. To what extent do the results for fruit flies apply to these myriad cases?

Also, the studies so far have focused on hovering flight, which is the hardest case to explain because the insect can gain no benefit from onrushing air. But do insects use other significant mechanisms to produce lift when they are moving? Many researchers are preparing to study these challenging questions. My group, for example, is building "bride of Robofly," which will live in a tank large enough for it to fly forward and make turns, to test, for instance, our hypotheses about how flies make their characteristic remarkably sharp turns by adjusting the timing of their wing strokes. After uncovering the basic set of tricks that insects use to stay in the air, the real fun now begins. SA

MORE TO EXPLORE

The Biomechanics of Insect Flight: Form, Function, Evolution. Robert Dudley. Princeton University Press, 2000.

The Web site of the author's research group is available at **http://socrates.berkeley.edu/~flymanmd/**

An account of the origins of the bumblebee myth is online at **www.math.niu.edu/~rusin/known-math/98/bees**