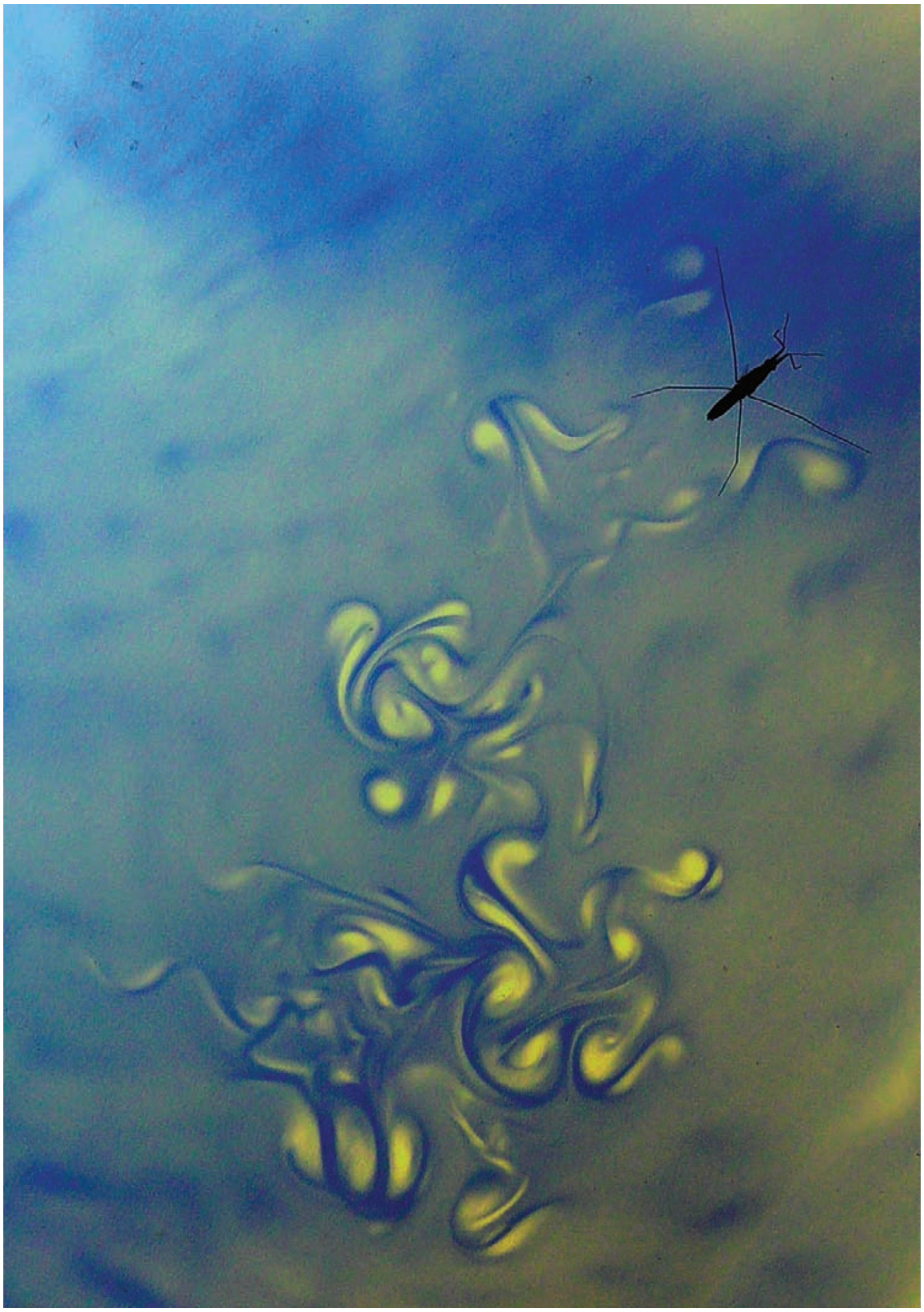


Trailing Vortices. *This photograph shows the vortices created by the water strider's legs as it moves across the water. Vortices are made visible by thymol blue. Bush has shown mathematically, and documented with photographs, that the vortices carry momentum backwards. By conservation of momentum, this makes the water strider move forward. (Photo courtesy of John W. M. Bush.)*

Fluid Dynamics Explains Mysteries of Insect Motion

Dana Mackenzie

WANTED: *Three miniature vehicles. Vehicle 1 should be able to hover in midair without going forward. It should not use a helicopter-like motion, but should instead beat its wings in an inclined plane, generating four times as much upward force as conventional aerodynamics predicts.*

Vehicle 2 should be able to walk on water. In fact, it should be able to sprint and jump when conditions demand. It should also be able to climb a frictionless slope, and do so without moving any part of its body.

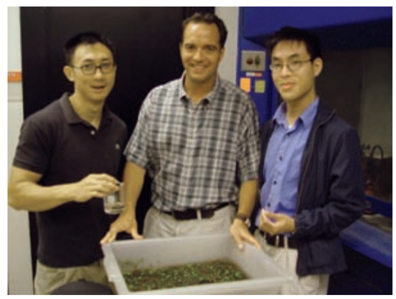
Vehicle 3 should be able to push itself through a highly viscous fluid and "fly" through a thinner fluid, and, moreover, it should be able to sense the difference between the two and adjust its method of locomotion accordingly.

All three vehicles should range in size from a few millimeters to a few centimeters. The winning designs should be backed up by at least 100 million years of field testing. Please submit proposals to . . .

No, this isn't a request for proposals from a real government agency, but the three "vehicles" described here do exist. Vehicle 1 is a dragonfly, Vehicle 2 is a water strider, and Vehicle 3 is an Antarctic mollusk known as the "sea butterfly." Together, their literally superhuman abilities show the vast differences between life at the scale of insects and life at a human scale.

"The world of water striders is dominated by surface tension. We live in a world dominated by gravity, so we have very poor intuition where surface tension is concerned," says John Bush, an applied mathematician at the Massachusetts Institute of Technology who has studied the motion of water-walking insects for about five years. Human intuition also fails to understand the hovering flight of dragonflies, which toss invisible vortices of air off with their wings as if they were tennis balls. We struggle also to imagine what life is like for the sea butterfly, which grows wings and uses them to "fly" through the water.

Bush and other applied mathematicians and physicists, such as Steve Childress of New York University and Jane Wang of Cornell University, are using mathematical methods (along with careful observation) to learn some of the secrets of the insects. Though his interest is purely fundamental, Bush says that engineers are beginning to take these lessons very seriously, as they try to design micro-air vehicles and microfluidic devices that will use the same mechanisms and operate on the same scales as the insects.



John Bush. *John Bush (center) with graduate students David Hu (left) and Brian Chan (right). (Photo courtesy of John W. M. Bush.)*

Hitting Their Stride

As you can see by taking a trip to a pond on a summer day, a water strider is a six- legged critter with a body about 1 to 4 centimeters in length and gangly legs that can make its total length closer to 20 centimeters. The legs are bent in such a way that a long piece, called the "tarsal segment," rests on the surface of the water. It acts like a snowshoe that distributes the bug's weight over a larger area and prevents it from breaking through the surface of the water. (See Figure 1.)

There is no great mystery about what holds the water strider up. As Bush said, it is the curvature force resulting from surface tension, which makes the surface behave like a trampoline. The strider's feet make little dents in the surface of the water, but as long as the force exerted by any foot does not exceed 140 dynes per centimeter, it will not and cannot break through. A quick calculation shows that, with a weight of 10 dynes distributed over a total tarsal length of about 10 centimeters, the water strider has a large margin of safety.

Figure 1. *An adult water strider, Gerris remidis. It is easy to understand how a water strider stands on the water: surface tension from the dimples in the water creates an upward force on the animal. However, until recently scientists have not been able to explain how the strider moves on the water. (Photo courtesy of John W. M. Bush.)*

But *moving* on water is another problem entirely. How can you walk on a surface that is practically frictionless? Why don't water striders slip and flail around like humans walking on a patch of ice? For a while, biologists thought they knew the answer. The same surface tension forces that hold the water strider up also provide a little bit of resistance to its movements. When the strider pushes against the water, it creates a little packet of "capillary waves" that move backwards and transport momentum with them. According to Newton's Law of conservation of momentum, if the wave momentum is carried backward, then the insect must move forward.

But there is a problem with this explanation, first pointed out by Mark Denny of Stanford University in 1994. Capillary waves in water have a minimum speed of 23.2 centimeters per second, which can be computed from the density and surface tension. But infant water striders, as shown in laboratory experiments, cannot move their legs that fast. That means they cannot generate capillary waves. No capillary waves means no momentum transfer and no fun for the juvenile water strider.

When he first read about Denny's paradox, Bush immediately saw one flaw in the argument: biologists were assuming the strider's leg traveled at a steady rate. It's true that a paddle traveling through water at less than 23 centimeters per second will not generate a capillary wave, Bush says. But the leg motion is not a steady straight-line motion; it is a short impulse followed by a return stroke. The theory of steady motions does not apply.

To see what was really happening, Bush's graduate student David Hu went out to Walden Pond to collect some water striders, bring them back and watch them walk. "From the very first day in the laboratory, it was clear that they were shedding vortices," says Bush. Vortices are a hallmark of unsteady fluid flow. Engineers and weather forecasters may hate them, but insects love them—and water striders wouldn't be able to go anywhere without them. The discovery of the vortices did not, of course, refute Newton's Law. The water strider still moves by means of momentum transfer, but it is the vortices, not the capillary waves, that do the lion's share of the work.

Eventually, Bush and Hu used a chemical dye called thymol blue to make gorgeous images of the vortices trailing away behind a moving water strider, just like the footprints of a rabbit through the snow. (See Figure "Trailing Vortices," p. 86.) Another student, Brian Chan, developed a robotic water strider, an ingenious contraption that Bush describes as "truly scientific research on a shoestring." The strider was powered by a piece of elastic thread taken from Chan's sock! Research groups at Carnegie-Mellon and Columbia University are now working on more sophisticated versions of Chan's Robostrider, with more powerful energy sources such as a solar cell. (See Figure 2, next page.)

The striders' ability to walk on water is but one of many amazing feats performed by water-walking insects. How do

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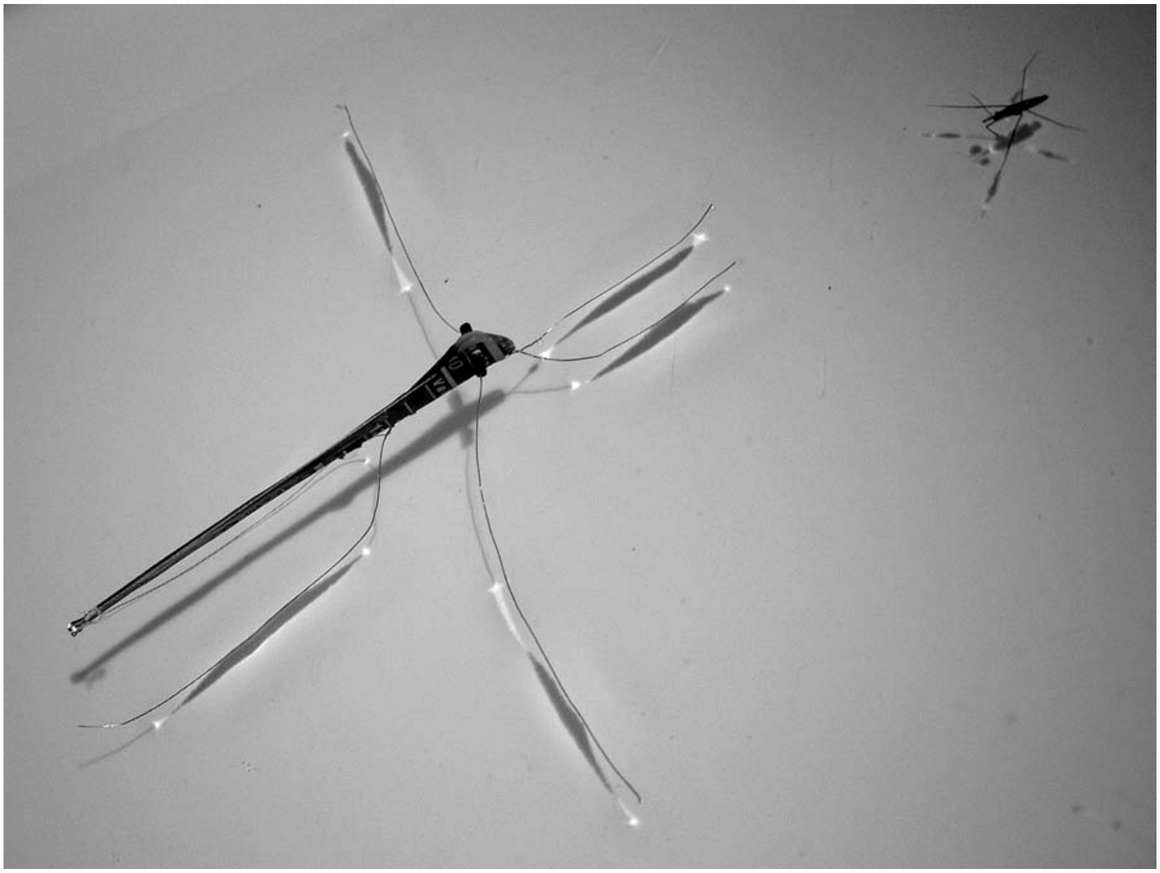

Figure 2. *Chan created a mechanical water strider, powered by an elastic thread from his shoelace, that could take a few steps before running out of power. Other scientists have since developed more sophisticated versions. (Photo courtesy of John W. M. Bush.)*

such insects get out of the water? As Figure 3 shows, an insect perceives the meniscus at water's edge very differently from us. To the insect, it is a frictionless hill that is taller than the insect itself, sloping up to a daunting angle of 40 degrees. If you imagine trying to climb a 40-degree slope of ice that is several feet high, you can begin to appreciate the water strider's problem.

Relatively large water-walking insects cheat by jumping to the top of the hill. Those that cannot jump apply a far more ingenious solution, which also relies on surface tension. For example, an insect called the water treader (*Mesovelia*) has miniature claws that are hydrophilic (water-attracting)—unlike the rest of the leg, which is hydrophobic (water-repelling). The treader plucks the water's surface up a little bit with its front claws, while pressing down with its middle claws. It holds this fixed posture, and in no more than a tenth of a second (so fast that it can only be seen with high-speed photography) it *accelerates* to the top of the hill!

What makes this trick work? It is the same principle that makes corn flakes stick together in a bowl of milk, or bubbles stick together in a glass of champagne. Whenever two menisci get close enough to each other, they tend to attract. The meniscus on one side and the insect's claws on the other side bend

Figure 3. *A water treader, Mesovelia, faces a seemingly impossible task. How can it climb a perfectly frictionless surface, slanted at an angle of 40 degrees, in order to get out of the water? Cheating (by grabbing the wall of the container) is not allowed. (Photo courtesy of John W. M. Bush.)*

the surface layer of the water into the shape of a "U". The water always tries to minimize its surface energy, and it does this by reducing its area. Thus a force is generated that pulls the two sides of the "U" together until they coincide. The force is quite a strong one—stronger than the gravitational force on the water strider—and so the whole thing is over in less than the blink of an eye.

Water-walking insects are not the only animals that use the meniscus trick. When a waterlily leaf beetle falls into the water, it curls its tail upward and lifts the surface of the water. It too glides up the meniscus in a fraction of a second. "They always go tail first, and I wonder if they do it to avoid concussions," Bush says, perhaps only partly in jest. (See Figure 4, next page).

Bush is now studying capillary feeding, which has been observed in birds: How can a bird suck a liquid up into its beak, when it can't pucker its lips to create suction? Some birds use surface tension: they draw a drop into the tip of their beaks; then, in its quest to minimize surface energy, the drop is drawn towards the bird's mouth. Bush believes that some insects may use similar capillary feeding techniques, but no one has observed them because it's too hard to see. Where surface tension is concerned, humans have a lot to learn from animals. "I love working in this area because you gradually come to the conclusion that any mechanism you can imagine that works is already out there," Bush says.

A Sea Change

Steve Childress is another mathematician who doesn't mind traveling a small distance to study fluid dynamics. In his case, the research took him to Antarctica, where he went with biologist Robert Dudley of the University of California, Berkeley, to study a small mollusk called *Clione antarctica*, or the sea butterfly.

When they got to McMurdo Station in November 2000, Childress and Dudley seemed to be out of luck. A cold spring had wiped out the anticipated "spring bloom" of sea butterflies.

Figure 4. *A waterlily leaf beetle, Pyrrhalta, demonstrates the solution to the meniscus-climbing problem. By arching its back, it creates curvature in the surface of the water. Surface tension then creates a strong horizontal force that allows it to reach the edge of the water even though it has to go "uphill." The water treader uses the same solution, except that it plucks the water surface upward with its forelegs and hind legs, while pushing down with the middle legs. (Photo courtesy of John W. M. Bush.)*

Childress and Dudley could not find a single adult—only juveniles. However, this disappointment actually was a stroke of serendipity because it forced them to pay serious attention to the juveniles for the first time.

Adult sea butterflies are about 1.5 centimeters long, but the juveniles are only 3 to 4 millimeters. They have a cigar-shaped body with stubby "wings," and, in addition, they have three bands of cilia roughly circling their head, waist, and tail. The cilia pose an interesting question. Why does one creature need two ways to get around?

In laboratory experiments, Dudley changed the viscosity of the water by adding chemicals to it, and observed how the sea butterfly larvae responded. When the water was more viscous, they would use their cilia to swim, and tuck their wings into their bodies. When the viscosity was reduced, out came the wings. "Dudley could almost train those creatures to stick out their wings and flap them," Childress says. Childress realized that what he was seeing was an adaptation to moving through two different kinds of fluid. Only in the natural setting, it isn't the viscosity of the water that changes—it's the size of the animal as it grows.

Birds propel themselves in a manner reminiscent of water striders, by flapping their wings and generating vortices of air.

Intuitively, the most important quantity for describing a fluid's flow is its viscosity. A viscous or "thick" fluid, such as molasses, tends to flow along smooth streamlines, with no vortices or turbulence. An inviscid or "thin" fluid, such as air, flows in a more complicated way, with lots of turbulence. But for a body moving through a fluid, the size and velocity of the body also play an important role. If the body is very small or moving very slowly, it will not generate eddies even in a thin fluid. Thus it is a combination of factors—the viscosity ν, the velocity u, and the length of the body L, that governs the fluid flow. These factors can be summed up in a combined parameter called the Reynolds number:

$$\mathrm{Re} = uL/\nu.$$

Thus, a 2-millimeter animal, moving through water, will experience the same Reynolds number as a 2-meter human moving at the same speed through a fluid that is 1,000 times more viscous than water—a very thick soup indeed!

In the regime of low Reynolds numbers, a well-known theorem of fluid mechanics, called the scallop theorem, says that you cannot propel yourself forward with any sequence of body configurations that is reversible in time. (Thus, wing-flapping or dolphin-kicking are ineffective.) However, it is possible to make forward progress with an asymmetric motion. For instance, you can row: press against the water with a flat paddle, then turn the paddle 90 degrees and move it back to its starting point in a way that minimizes drag. Most sub-millimeter sized animals use a different method. They have cilia or flagella that propel them through the water with a corkscrew motion. This is consistent with the scallop theorem because the time reversal of a left-hand screw is a right-hand screw, which is distinguishable from the original motion.

At high Reynolds numbers (say, $\mathrm{Re} > 1,000$), a whole different set of principles comes into play. This is the realm of bird flight, and at even higher Reynolds numbers ($\mathrm{Re} > 1,000,000$), airplane flight. Mathematicians understand high Reynolds numbers very well. Birds propel themselves in a manner reminiscent of water striders, by flapping their wings and generating vortices of air. As they push the vortices backwards, they receive an equal amount of forward momentum. Thus the main purpose of flapping is to provide thrust. In an airplane the thrust is produced in other ways—for example, by propellers—and the function of the wings is to provide lift (for which purpose a fixed wing is sufficient.)

Most animals, though, live in the intermediate zone between low and high Reynolds numbers, where the equations of fluid mechanics, called the Navier-Stokes equations (see "Vortices in the Navier-Stokes Equations," p. 78) are not as easy to analyze. The sea butterfly juveniles start at a Reynolds number of 10 and grow to a Reynolds number of 100 or so. Through Dudley's experiments, Childress discovered that the sea butterflies' swimming speed while flapping slowed down at the lower Reynolds number, and (when extrapolated) vanished at a value of about 12. This indicated a finite, nonzero threshold for flapping flight. As the Reynolds number increases, flapping becomes more and more efficient.

It appears that sea butterflies have discovered a theorem that mathematicians were not aware of. The scallop theorem (which says that flapping has zero efficiency) has been proved only at a Reynolds number of 0, but the sea butterfly data strongly suggests that a bifurcation takes place around Reynolds number 12. Below this number, a flapper may jiggle around randomly but it won't be able to move. It is trying to create vortices, but the vortices diffuse away before they can generate thrust. Above this number, a spontaneous symmetry-breaking occurs. Any little push on the animal will create a fore-aft asymmetry, and the fluid is now thin enough that the animal can exploit it. When it flaps its wings, the fore-to-aft fluid flow will carry the eddies away before they disperse. The animal can now fly. (See Figure 5.)

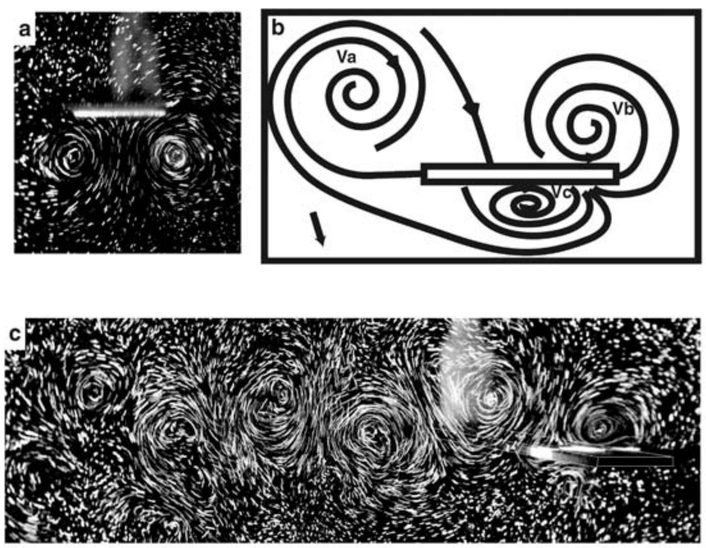

Figure 5. *(a) At low Reynolds number, a flapping wing cannot generate propulsion because it generates symmetric fore and aft vortices. (b) However, at a certain threshold value of the Reynolds number, the symmetry breaks spontaneously. (c) Above the threshold value, flapping flight becomes feasible. Note that the mechanism of propulsion is the same as that of the water strider: flapping creates vortices that carry momentum backward, allowing the animal to move forward. (Figure courtesy of the Applied Mathematics Laboratory, Courant Institute of Mathematical Sciences.)*

So far, no human mathematician has proved the "sea butterfly theorem" yet. Childress verified it for a simplified version of the Navier-Stokes equations, called the Oseen model (see "Vortices in the Navier-Stokes Equations," p. 78), which ignores the feedback between a moving body and the surrounding fluid. (In the Oseen model the flow of the fluid affects the motion of the body, but not vice versa.) For a flapper based on the shape of the sea butterfly, he estimated that the bifurcation occurs at Reynolds number 36. Due to the simplifying assumptions of the Oseen model, that number is clearly an overestimate, but it is a proof of principle that the bifurcation exists. "Nature has probably smoothed out the dividing line by being clever, but what we've done is make it very precise," Childress says.

Dragonflies and Falling Paper

In the late 1990s, when she was a NSF-NATO Postdoctoral Fellow in physics at Oxford University, Jane Wang went to the library to look for a book on random matrices. What she found instead was a new direction for her career. She happened to pick up a book by Childress, called *Mechanics of Swimming and Flying*. "What a fascinating thing to study!" she thought. Later she worked on a postdoctoral project with him, and now she has become one of the leading researchers on the mathematics of insect flight. Recently she proposed a new theory of how dragonflies manage to hover in place.

To watch a dragonfly is to be amazed at its ability to stop and start in midair; even other hovering animals, such as hummingbirds, don't seem to have quite the same precision of movement.

To watch a dragonfly is to be amazed at its ability to stop and start in midair; even other hovering animals, such as hummingbirds, don't seem to have quite the same precision of movement. Staying airborne without moving forward has always been a challenging aeronautical problem. Fixed-wing aircraft and most birds can't do it because their lift results directly from the flow of air past the wing. Helicopters make do with a rotating wing. Hummingbirds, like helicopters, rotate their wings in a mostly horizontal plane, deriving lift from the flow of air past the wings.

The conventional "lift coefficient" of a wing reflects the dependence of a wing's lift on its airspeed. An ideal two-dimensional wing develops a lift L that is proportional to the square of the wing's speed u, the density of air ρ, and the wing's cross-sectional area S. Specifically, the lift is given by the formula:

$$L = \frac{1}{2} C_L \rho u^2 S$$

where C_L, the lift coefficient, equals $2\pi \sin\alpha$, and α is the "angle of attack" of the wing. Thus a horizontal wing (in theory) generates no lift. A wing improves its lift by tilting slightly, so that $\alpha > 0$. However, if it tilts too much, it stalls (which means that the flow of air off the trailing edge is no longer smooth). In practice, this typically occurs around $\alpha = 15^\circ$, so the lift coefficient hits its maximum value somewhere between 1 and 2.

Dragonflies are puzzling to a physicist for two reasons. First, their wings do not move in a nearly horizontal plane, but a steeply inclined one. Second, the first estimates of the lift coefficient of their wings seemed to be about four times too large to be reasonable—between 3.5 and 6. Of course, there are several problems with applying the aerodynamic formulas for aircraft to the wings of a dragonfly. Those formulas assume a steady state—a fixed wing moving at constant speed through a fluid. But a steady-state model doesn't apply to dragonflies, just as it did not apply to John Bush's water striders. The anomalous lift of the dragonfly wings may come in part from their ability to generate vortices and propel them downward. This almost certainly seems to be the case for many insects, from fruit flies to hawkmoths. (See Figure 6, next page, and see Figure 7, p. 97.)

However, Wang found an even more important mistake in the conventional analysis of dragonfly flight. Every wing generates drag as well as lift. Drag is the force parallel to the wing's

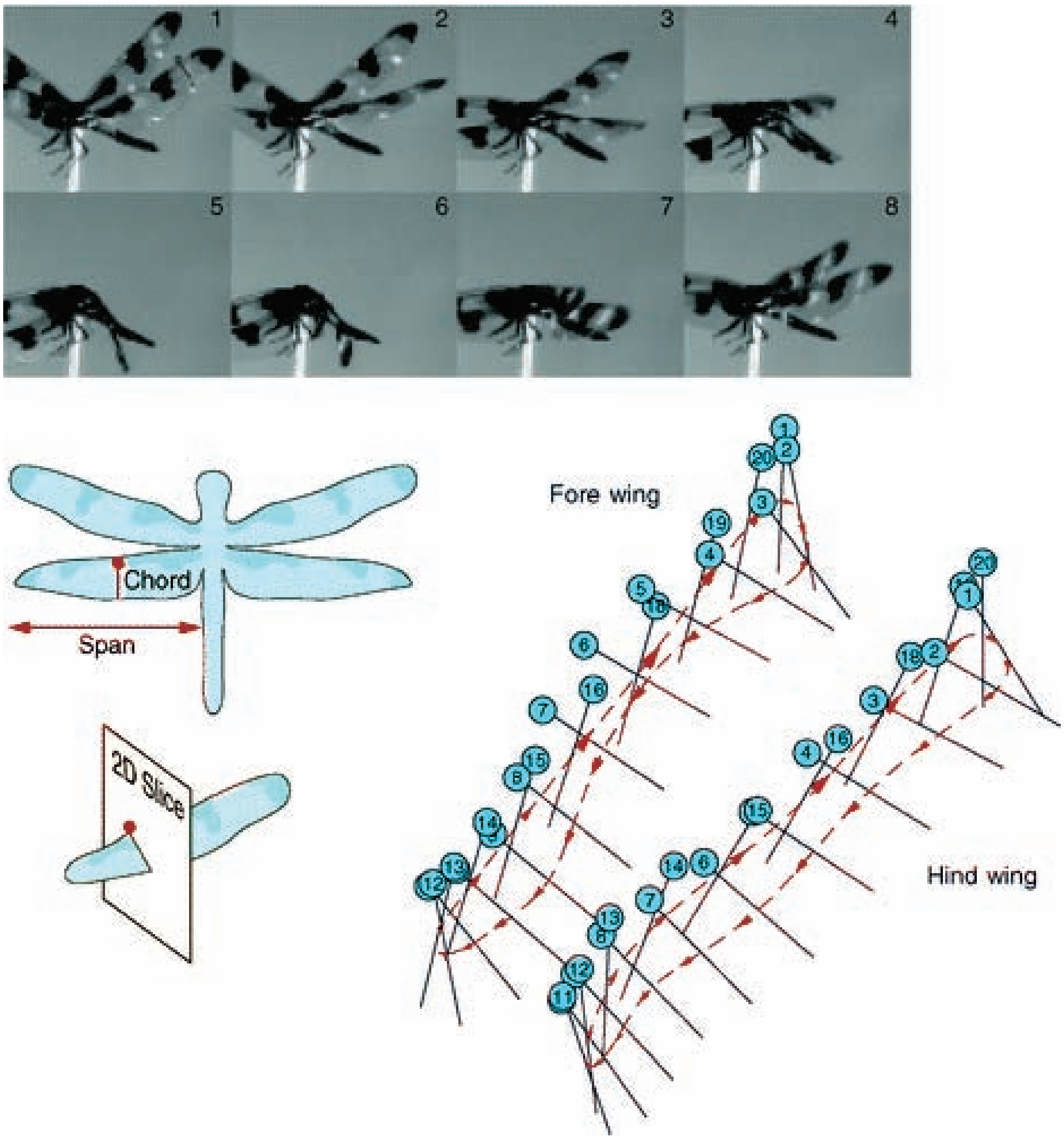

Figure 6. *Hovering flight of a dragonfly posed theoretical problems because the dragonfly wing appears to generate more lift than any known airfoil. In this sequence of pictures, note the steep slope of the downstroke (inclined at 60 degrees), which Jane Wang says is optimal for hovering flight. (Reprinted, with permission, from the Annual Review of Fluid Mechanics, Volume 37, © 2005 by Annual Reviews, www.annualreviews.org.)*

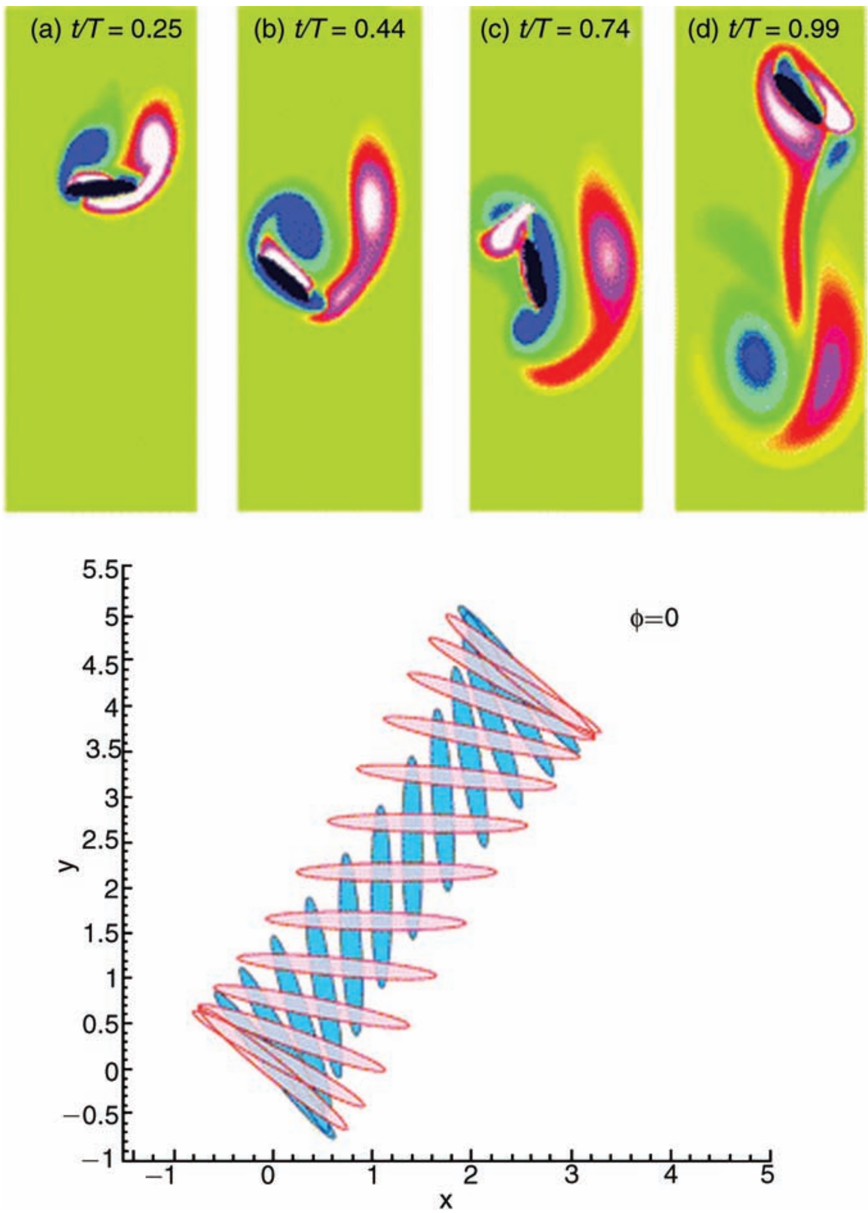

Figure 7. *Like the water strider and the sea butterfly, the dragonfly creates vortices and propels them in the opposite direction from the way it wants to go. (Reprinted, with permission, from the Annual Review of Fluid Mechanics, Volume 37, © 2005 by Annual Reviews, www.annualreviews.org.)*

As the wing is moving downward along this path, aerodynamic drag resists its motion—and therefore the drag has a very large upward component. It would be absurd for the dragonfly to minimize drag, because the drag is helping it out!

motion, while lift is the force perpendicular to the motion. To an aeronautical engineer, drag is always bad because it slows the plane down and contributes nothing to keeping the plane aloft. Engineers always try to keep the lift-to- drag ratio as high as possible. Previous researchers had assumed that the dragonfly wing must also have a high lift-to-drag ratio.

However, that turned out to be incorrect. In high-frequency photos, Wang could see that the dragonfly, when hovering, beats its wings along a steeply inclined path, which makes a 60-degree angle with the horizontal. Because the animal does not have any forward component of velocity, the 60-degree inclined plane marks the true direction of motion of the wing. As the wing is moving downward along this path, aerodynamic drag resists its motion—and therefore the drag has a very large upward component. It would be absurd for the dragonfly to minimize drag, because the drag is helping it out! The dragonfly therefore turns its wing to press against the air like a paddle, creating an angle of attack around 60 degrees and producing lots of drag. On the other hand, during the upstroke, the drag will point downward. On that part of the stroke, the dragonfly does want to minimize drag, so it turns it wing parallel to the airflow to reduce the drag force. (See Figure 8.)

Because the angle of attack of the wing is so large, it is very far into the stalled regime. Any analysis of its motion based on smooth, steady fluid flow is bound to give incorrect answers. So Wang went back to the full Navier-Stokes equations and worked out a model that incorporates both lift and drag. The model showed that 76 percent of the vertical force on the dragonfly's wing comes from drag. In other words, the force is almost exactly 4 times greater than it would be if the wing were using lift alone. This completely resolves the problem of where the dragonfly gets its "extra" lift from. Computer simulations also showed that the wing tosses vortices downward, so that in fact the way a dragonfly stays aloft is very reminiscent of the way a water strider moves forward. Finally, the simulations demonstrated that the vertical force due to drag decreases sharply if the plane of motion of the dragonfly wing gets steeper than 60 degrees, because of the effects of unsteady flow (the interaction between the wing and the flow generated in the previous stroke). So it seems to be no accident that dragonflies beat their wings at that angle.

Wang and her students are currently trying to determine optimum wing-motion patterns for several other kinds of flying animals, including fruit flies, hawkmoths, and bumblebees. So far they are finding that the optimal beating frequencies and wing trajectories are close to the ones that the animals actually use. Once again, nature seems to have figured out the best possible solution long before mathematicians did. However, without mathematics we certainly would not be able to appreciate the efficiency of the solutions that nature has evolved.

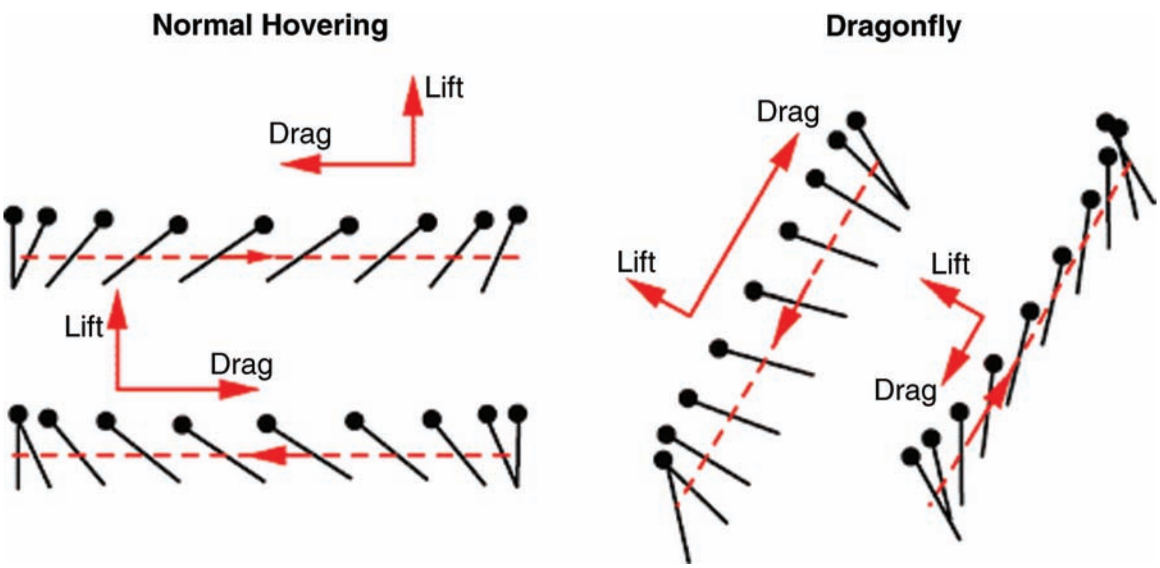

Figure 8. *Hummingbird hovering and dragonfly hovering may seem similar, but the physical mechanisms are quite different. Hummingbird wings move in an essentially horizontal plane; thus, the hummingbird stays aloft by lift alone. Dragonfly wings operate in a "highly stalled" regime, which is bad for hummingbirds and airplanes but perfect for dragonflies. They use both lift and drag to stay aloft. Note also that the horizontal orientation of the wing during the downstroke creates maximal drag. On the upstroke, the dragonfly orients its wing vertically to minimize drag. (Reprinted, with permission, from the Annual Review of Fluid Mechanics, Volume 37, © 2005 by Annual Reviews, www.annualreviews.org.)*