

Caught on camera

By recording animal movements that are too fast for the human eye to follow, high-speed digital video is transforming studies at the interface of biomechanics, neuroscience and evolutionary biology. Rex Dalton reports.

One spring day last year, deep in the lush tropical cloud forest of Ecuador's Maquipucuna Reserve, Kimberly Bostwick positioned herself on the side of a ravine to observe an avian mating show in the upper canopy. Pulling out her new high-speed video camera, she waited for the brightly coloured actors: male club-winged manakins (*Machaeropterus deliciosus*).

Ornithologists knew that the male manakin makes a musical humming sound with its wings as part of its mating ritual¹, but no one had ever seen exactly how it was done. Bostwick's camera captured for the first time one of the birds clapping its wings behind its back at blinding speed. "It brought tears to my eyes," recalls Bostwick, now a curator of ornithology and mammalogy at Cornell University's Museum of Vertebrates in Ithaca, New York. "It was so gorgeous."

Frozen in time

Bostwick's video observations, contained within the doctoral thesis she completed at the University of Kansas in May, are part of a new wave of studies made possible by the relatively inexpensive, portable, high-speed cameras that have hit the market in the past few years. They have made it possible to take freeze-frame studies of lizards running on water, flies beating their wings, cockroaches scuttling over obstacles and fish gliding through water. By integrating this information with electrophysiological recordings,

researchers are gaining previously inaccessible insights into animal movement and its neural control. "We are creating a new field of neuromechanics," says Robert Full, who studies animal locomotion at the University of California, Berkeley.

Evolutionary biology is another beneficiary. For Bostwick and her Kansas supervisor, Rick Prum, the cameras have shed light on the importance and intricacies of sexual selection, the evolutionary mechanism involving competition between males and mate choice by females that Charles Darwin proposed can operate alongside natural selection.

In 1871, Darwin wrote about sexual selection as a driving force for the evolution of mechanical sound production by birds². Manakins are the most extreme example, the males having evolved flattened wing bones and thick-tipped feathers to facilitate their sonic displays. Bostwick's video observations have now revealed that sexual selection has pushed the mechanics involved to the physiological limit: the birds' wings move back and forth almost as fast as muscle cells can contract. "The feathers hit behind the back 120 times per second," says Bostwick.

Rapid response

Just five years ago, a camera system to shoot this event at the required speed and light settings would have cost more than US\$30,000. "And they were almost impossible to work with in the field," says Bostwick. The camera she used, a MotionMeter manufactured by Redlake of San Diego, California, can shoot up to 1,000 frames per second. The hand-held device gives instant frame-by-frame playback and costs about \$10,000.

George Lauder, an evolutionary biologist now at Harvard University, was the first to explore the potential of high-speed cameras in mechanical studies of animal movement in the mid-1980s. Working at the University of California, Irvine, Lauder and his colleagues photographed fish swimming against a current in a flow tank, initially using old-fashioned film. As a result, their progress was limited by lengthy delays for film processing.

High-speed digital video has changed all



By suspending fruitflies on a wire, researchers can photograph their beating wings — but they remain a blur (above). High-speed video is now bringing this motion into focus.

that. "It has revolutionized the ability to see what animals are doing in a fluid environment," says Lauder. Today, his only real bottleneck is storing the vast quantities of data that his cameras generate. "An eight-second sequence of video fills a compact disc," Lauder explains. "We video with two machines at once. So we are burning CDs for two days after our experiments."

Lauder and his colleagues shine lasers on swimming fish to study the movement of both the fish and the surrounding water,



In the frame: video images reveal how green basilisks manage to walk across water.



which is revealed by the presence of tiny suspended glass beads that catch the light. Using this method, Lauder has, for instance, measured the forces involved in the doughnut-shaped vortices that form around the pectoral fins — behind the gills — of the bluegill sunfish (*Lepomis macrochirus*), in which the flow loops round before jetting through the doughnut's centre³.

By repeating their studies with fish from primitive sharks, through intermediate forms such as sturgeon, to the most advanced species, including the sunfish, Lauder and his colleagues hope to understand how complex mechanisms of aquatic locomotion have evolved and diversified.

Joint effort

Neuroscientist Roy Ritzmann of Case Western Reserve University in Cleveland, Ohio, is another enthusiast for high-speed video. He learned of its potential while serving on a panel reviewing one of Lauder's grant applications. Ritzmann now uses similar cameras to study deathhead cockroaches (*Blaberus discoidalis*), and has found that there is much more to the creatures' scuttling motion than meets the eye. "Each leg has a different function," says Ritzmann. "When the animal is moving, the joints are doing different things — legs are reaching out, pushing or pulling. It is really a complex situation."

Most recently, Ritzmann has watched roaches climb over obstacles in their path. The video stills reveal how the insects rotate the joints of their middle pair of legs to achieve the rearing necessary to clear the obstacle⁴, and electrophysiological recordings from the roaches' leg muscles have begun to reveal how this movement is controlled⁵. Ritzmann now plans to video cockroaches in which specific neural circuits have been disabled, to gain further insights into the processes involved.

Ritzmann's findings are fascinating from a purely biological standpoint, but they are also stimulating the field of robotics. His data are being studied by Roger Quinn and his colleagues at Case Western's Biologically Inspired Robotics Laboratory, who are building insect-like six-legged robots. For more than a decade, Quinn's group has tried to translate the roach's ability to traverse complex terrains to a mechanical device. "We are developing our fifth generation of robot — getting closer and closer to a cockroach," says Quinn.

Whereas Lauder and Ritzmann focus on



In a flap: Kimberly Bostwick has used high-speed video to show how male manakins clap their wings to generate a humming sound.

movement in water and on land, Michael Dickinson of the University of California, Berkeley, is using high-speed video to study flight. To analyse the flight of fruitflies and blowflies, arguably nature's most stunning flying machines, Dickinson and his colleagues have used a Kodak EktaPro camera that can shoot 3,000 frames a second.

Each cycle of wing movement has four components: upstroke, downstroke and two rotational phases, called pronation, which occurs after each upstroke, and supination, after each downstroke. By slowing down these movements using high-speed video, and then measuring the forces involved using the 'Robofly', a mechanical device that simulates a fly's wing movements in a vat of oil, Dickinson and his colleagues are uncovering the mysteries of insect aerodynamics.

Creating a buzz

They are currently trying to determine the forces involved when a fruitfly makes a rapid right-angle turn during flight, known as a saccade. A fly inside a cage is coaxed through a 'vision field' — a cube about seven millimetres square — where three high-speed video cameras capture its movement from different angles. The film is then slowed down, the wing and body movements are identified, and this knowledge is transferred to the Robofly, which then mimics a saccade and allows the forces involved to be measured. "Without high-speed video, we couldn't measure what the fly is doing," says Dickinson.

In other experiments, Dickinson and his colleagues have tethered blowflies (*Calliphora vicina*) with microscale electrodes implanted in 'steering' muscles that can subtly alter the plane and amplitude of each wing stroke.

They have found that the precise timing of spikes of activity in these muscles is the key to the flies' extreme manoeuvrability^{6,7}. "The video allows us to decode what the flight system is doing," says Dickinson, who will soon move to an expanded lab at the California Institute of Technology in Pasadena. "It has changed my view of biology."

In addition to bringing such fundamental insights, high-speed video is demystifying some of nature's quirks. Green basilisks (*Basiliscus plumifrons*), indigenous to Costa Rica, Nicaragua and Panama, are known as 'Jesus Christ lizards' for their ability to scamper across water. By shooting video at 250 frames per second, Tonia Hsieh, a graduate student in Lauder's lab, is investigating how they do it. "We are trying to figure out how locomotion changes on different surfaces," says Hsieh. "There is a huge body of literature on locomotion on the ground, but little on water and sand."

By videoing particles suspended in the water, Hsieh has examined the wake produced by the lizard's feet — which provided data on the vortices created, the force of impact of the feet on the surface and the forces exerted as the feet push backwards. At the Society for Integrative and Comparative Biology meeting in Anaheim, California, in January, she revealed that the forces that prevent the lizards sinking are generated by pushing the feet back and inwards, rather than back and outwards, like most lizards running on land.

This method allows young basilisks to stay above the surface — the largest that Hsieh has filmed running on water weighed 78 grams. But at 200 grams, adult basilisks no longer have their miraculous powers.

As more researchers begin to experiment with the new digital cameras, expect further wonders to emerge from nature's high-speed blur. Ritzmann likens the technology's current impact on organismal biology to that of electron microscopy in cell biology some three decades ago. "It allows you to see things never imagined before," he says. "It's almost like cheating." ■

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