

Symmetry in Turns

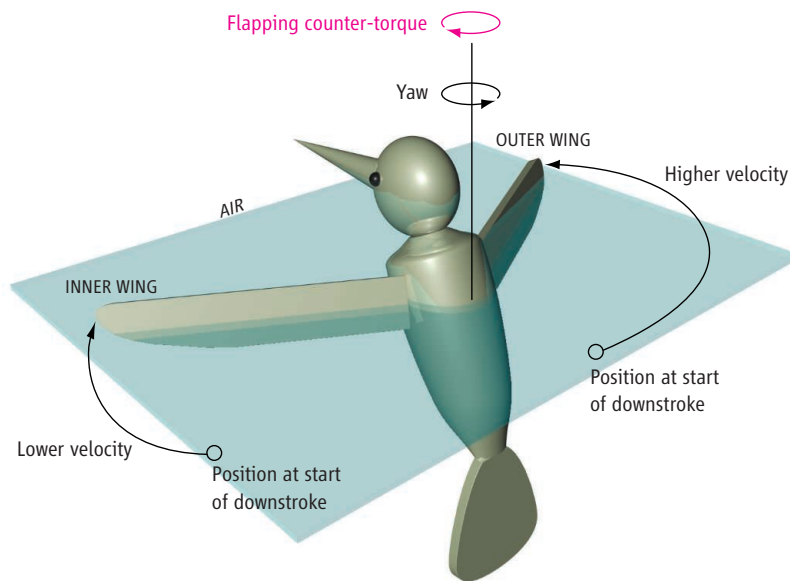
Bret W. Tobalske

Being earthbound save for the ability to fly airplanes and helicopters, humans stand in awe of animals that power their own movement through the air by flapping their wings, and of the spectacular maneuvers that some of these animals can achieve. Imagine a common housefly flying in tight, erratic circles as it attempts to escape from a room or a hummingbird diving and turning to chase a competitor away from a backyard feeder. One might expect these extreme maneuvers to be accompanied by pronounced asymmetries in the way animals move their wings. Yet, evidence from insects (1, 2), birds (3, 4), and bats (5) suggests that aerial maneuvers are routinely accomplished through

relatively subtle changes in wing motion. On page 252 of this issue, Hedrick *et al.* provide further insight into this phenomenon (6). The results will inform all future research into maneuvering flight in animals and biomimetic flying robots.

The authors show that flying animals arrest yaw (rotation about a vertical axis; see the figure) during hovering and slow flight by spinning about a vertical axis, without asymmetry in their wing movement. Holding both wings with the same posture, and flapping them back and forth in the same way relative to their body, are sufficient to stop the spinning. The authors refer to the underlying phenomenon as “flapping counter-torque.”

To understand the importance of this result, consider the array of solutions that flying animals have at their disposal to modulate aerodynamic forces (lift and drag) and inertia (mass and its distribution). Animals may vary the velocity of their wings by increasing the frequency and amplitude of their wingbeat, alter the path of wing movement relative to the body, or twist the whole wing to alter the angle at



Flapping counter-torque during a yaw maneuver. The hovering bird is engaged in downstroke and is yawing counterclockwise about a vertical axis. Coupling the overall rotation of the body with symmetric motion of the wings causes the outside wing to move faster than the inside wing relative to air. The outer wing thus generates greater aerodynamic force, and a net flapping counter-torque (red) decreases the rate of yaw (6).

which it meets the air. Birds or bats may also use their muscles and internal skeletal elements to alter wing curvature, surface area, or long-axis twist (1–8). Testing which—if any—of these features are being altered requires multiple, synchronized high-speed video recordings to reconstruct motion in all three dimensions.

Once a yaw is initiated, either by a force external to the animal (for example, from a gust of wind) or by an asymmetry in force production created by the animal’s wings, some form of force asymmetry is necessary to arrest the yaw. If yaw is occurring counterclockwise as in the figure, a net clockwise torque (force times distance from the axis of rotation) is required to stop the yaw. Hedrick *et al.* develop a mathematical model that predicts how symmetrical wing flapping can create such a torque.

In their model, during downstroke (see the figure), both wings move at the same velocity relative to the bird, but in terms of global motion relative to Earth and air, the outside (right) wing moves faster than the inside (left) wing, because the angular velocity of the body adds to the angular velocity of the outside wing and subtracts from the angular velocity of the inside wing. Because lift and drag on the wings are proportional to

A model explains how animals maneuver during hovering and slow flight.

velocity squared (9), the outer wing exerts an exponentially larger force on the air. The orientation of net force is nearly perpendicular to the upper surface of each wing (2), and the difference in force between the wings generates a net clockwise torque that decelerates the angular velocity of the body. The process is reversed during upstroke (see Hedrick *et al.* for details).

Hedrick *et al.* use the predictions of yaw deceleration from the above model to test the model’s validity against an alternative model that incorporates active modulation of wing posture and motion. They then compare the predictions of both models to video recordings of maneuvers in four

species of insects, two bird species, and a bat. According to their model, symmetrical flapping causes an exponential rate of decay in yaw velocity, whereas active modulation of wing posture and motion creates a linear rate of decay in yaw. All animals exhibit exponential decay in yaw.

The fact that the flapping counter-torque model is robust over a wide range of body size indicates that it represents a universal model. This advances our understanding, because previously it was thought that maneuvers in small insects would be dominated by skin friction due to the viscosity (“stickiness”) of the air (2) and in larger birds and the bats by wing and body inertia (3, 4). The relative contribution of inertial force over viscous force is expressed as a Reynolds number: The higher this number, the greater the extent to which body and wing inertia dominate aerodynamics (9). The largest bird Hedrick *et al.* studied has a Reynolds number 148 times as large as that of the smallest insect in their sample; yet each used the same mechanism—flapping counter-torque—to arrest their yaw.

Hedrick *et al.* hypothesize that flapping counter-torque may simplify the neural input that would otherwise be required to recover from perturbations during flight. This predic-

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tion may lead to new research into the neuromuscular control of aerial maneuvers in animals (3, 4) and will aid efforts to engineer controllers and actuators that effect wing movement in biometric flying robots (10). Passive stability during flapping may thus be analogous to a process in terrestrial locomotion in which neural input and passive dynamics interact to augment stability (11).

A major goal of functional morphology and comparative biomechanics is to understand how animal design relates to movement, ecology, and behavior. Thus, it is also important that Hedrick *et al.* show that animals with wings that are large relative to their body size decrease yaw velocity more quickly than animals with proportionally small wings.

Hypotheses about maneuverability and ecomorphology in birds and bats have been dominated by the assumptions of fixed-wing, gliding aerodynamics (12). It has been recognized for some time that flapping must be integrated with such models (3), and the model of Hedrick *et al.* is a vital step in this direction.

Yaw during hovering and slow flight is just one type of maneuver; an almost limitless array of combinations of yaw, pitch, roll, and flight velocity are available to flying animals. Now that technology has developed to the point where detailed measurements of flapping maneuvers have become feasible (1–8), a world of comparative research is opening in which the flapping counter-torque model can be used to test the functional significance of

flapping motions in maneuvering dynamics.

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GENOMICS

Green Evolution, Green Revolution

John M. Archibald

The trees and plants that color our continents are more closely related to aquatic microorganisms—unicellular algae, in particular—than they are to the animals and fungi with which they cohabit. The smallest of these algae, called picophytoplankton, are individually minuscule (less than 2 μm in diameter) but collectively massive in ecological and evolutionary importance. On page 268 of this issue, Worden *et al.* (1) present the genome sequences of two such microbes, which belong to the green algal lineage *Micromonas*. Their analyses provide crucial insights into the plasticity of the eukaryotic genome over short evolutionary time scales and also shed light on the genetic “toolkit” that may have been present in the ancestors of today’s land plants and green algae.

We are in the midst of a revolution in our exploration of the hidden microbial majority on Earth. Even the tiniest of cells can now be probed, poked, and sorted, and, with a bit of effort, subjected to DNA sequence analysis (2). In the case of photosynthetic eukaryotes, two microalgal genome sequences were available in 2004 (the diatom *Thalassiosira*) and the red alga *Cyanidioschyzon*); by early 2009, almost a dozen

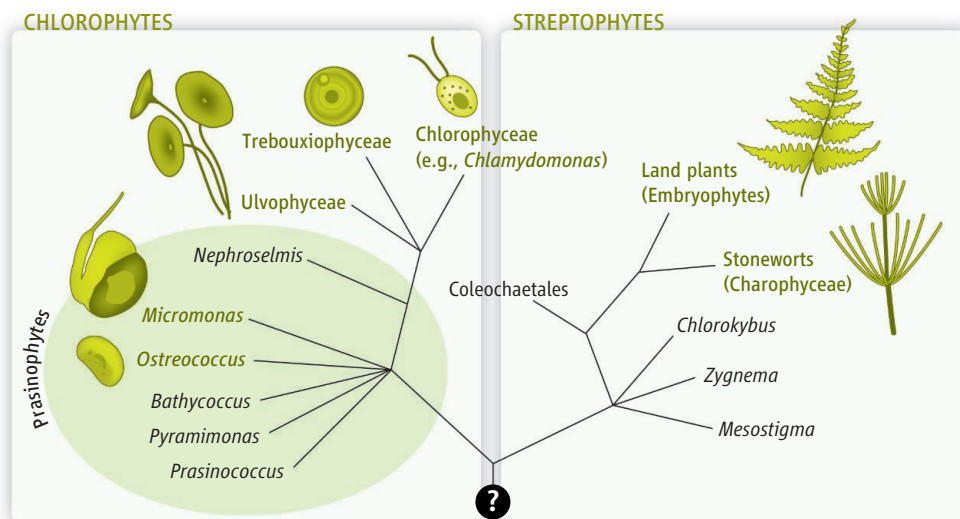
had been sequenced (3). Several of these sequences are derived from organisms within the green lineage, such as the model lab alga *Chlamydomonas* (4), providing valuable reference points for comparison to the genomes of land plants like *Arabidopsis* (5).

Green photosynthetic eukaryotes are divided into two branches, chlorophytes and streptophytes (see the figure). The streptophyte branch is composed of land plants and their closest relatives, such as stoneworts (6) and the aquatic unicell *Mesostigma* (7, 8). Molecular data [for example, (9)] show that

The genomes of two species of green algae provide clues to how green plants evolved.

the prasinophytes are the earliest offshoots of the chlorophyte branch; in the eyes of many, these organisms represent our best guess as to what the ancestor of green eukaryotic life looked like (10). It has long been hoped that a solid understanding of prasinophyte biology would open a window on the chlorophyte-streptophyte common ancestor.

The first prasinophyte genomes to be sequenced were from a pair of *Ostreococcus* species (11, 12), the reigning champions of eukaryotic cellular miniaturization (13). *Ostreococcus* genomes, too, are tiny: Just ~13



Green revolution. This evolutionary tree depicts a consensus view of the green tree of life, based on (10) and with consideration of new data, for example, from (8). By sequencing the genomes of two prasinophytes, Worden *et al.* (1) expand our knowledge of the genes present in the ancestors of land plants and green algae.