insecticide attacks. Alternatively, the good chemical sense might be a means of sensory compensation. *Tribolium* are adapted to fairly low light environments, which is reflected in their comparatively small eyes and also at the genome level by the fact that they possess only two opsin genes as opposed to three in most other insects. Thus, improved chemosensation may make up for the lack of optical sensory input due to the cryptic environment of this species.

It may be naïve to expect revolutionary insights into the biological peculiarities of a species from its genome sequence alone, but the genome sequence can in a sense help to refocus on the species itself. It may thus be seen as a reminder of how some problems that naturally have to be studied as isolated phenomena might interact and inform each other. The genome might thus help to focus on the species itself as a product of evolution, whose traces can be read from the genome. Only much further work — now able to draw on the resource of the *Tribolium* genome sequence — will reveal whether the genome holds an explanation for why evolution was so fond of beetles.

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Animal Locomotion: A New Spin on Bat Flight

Biologists and engineers have long struggled to understand the hovering flight of insects, birds, and bats. The enormous diversity of these groups would suggest they fly using a variety of mechanisms, but a new study shows that hovering bats use the same aerodynamic mechanisms as do moths and other insects.

Michael Dickinson

Active flight has evolved within just four taxa in the history of life: insects, pterosaurs, birds and bats. The ecological advantages of flight are manifest in the extraordinary success of these groups. Insects, birds, and bats include about 10^6, 10^4 and 10^3 species, respectively — together, the vast majority of described animal species on the planet. Even the ill-fated pterosaurs exhibited a diversity comparable to that of modern birds [1], with species ranging in size from sparrows to small aircraft. In addition to powerful muscles and an adequate control system, active flight requires aerodynamically effective wings [2]. Because of the multiple origins of flight, wings have long served as textbook examples of evolutionary homology and convergence. The wings of pterosaurs, birds and bats are homologous because they all originated from tetrapod forelimbs, whereas the wings of insects — probably derived from tiny dorsal extensions of the legs [3] — are convergent analogs. In comparing animal wings, it is possible to consider not only morphology and phylogeny, but also the aerodynamic mechanisms by which they work. A recent study of bats [4] suggests that hovering insects, birds and bats may use physical mechanisms that are more similar than previously supposed, and in doing so illustrates how common physical laws can drive distantly related creatures to similar solutions.

A coherent understanding of animal aerodynamics has been long coming, largely because the principles that explain how fixed-wing aircraft work are not sufficient to explain the flapping flight of birds, bats, and insects. Of the three, the forward flight of birds is the easiest to explain, because their wings function to some degree as do those of an airplane. If you place a bird wing in a wind tunnel, the forces one measures are usually sufficient to explain how flapping birds offset their body weight and fly forward through the air. This is not to say that bird flight is fully understood [5], but at least it makes sense in the context of conventional aerodynamics.

Understanding insect aerodynamics has proven more challenging. If one places an insect wing in a wind tunnel, the forces measured are typically much too low to explain how an animal gets off the ground. This exercise assumes that as the wing flaps back and forth it functions at each moment as it would under steady-state conditions. The failure of this so-called 'quasi-steady' model for many insects was elegantly summarized by Charles Ellington [6] in an influential 1984 monograph. This work helped foster a search for various unsteady mechanisms — ways that a flapping wing might create greater force than it does when held rigidly in a wind tunnel [7].

An important hint appeared in a 1979 paper by Tony Maxworthy [8], who used dynamically scaled model wings to study an unsteady mechanism called the 'clap and fling'. (Another pioneer of animal flight studies, Torkel Weis-Fogh [9], had suggested that the wings of tiny insects might create elevated forces as they fling apart at the start of each stroke.) Dynamic scaling operates on the principle that certain physical phenomenon — such as the flow of fluid around a flapping wing — are scale-independent as long as certain force ratios are conserved. In the case of hovering flight, the critical factor is the Reynolds number (*Re*), the ratio of inertial to viscous forces, which is equal to the velocity of wing motion times wing length divided by the kinematic viscosity of the surrounding fluid. By choosing values of size, speed and viscosity that maintain the same *Re*, researchers can study the aerodynamics of small, fast flapping wings on conveniently large, slow moving models. Maxworthy noted that, as the model wings started to move apart, they each created a prominent swirling flow called a leading edge vortex. Subsequent studies using dynamically scaled wings equipped with force sensors indicated that the lift generated by leading edge vortices is indeed sufficient to explain the forces required to hover [10,11]. In 1996, Charles Ellington's group [12] used a smoke rake in a wind tunnel to visualize a leading edge vortex on a large tethered hawk moth, indicating that real insects do indeed create these flow structures. Most hovering insects sweep their wing in one direction, creating a leading edge vortex, flip the wing over, and move it back in the opposite direction to create a new leading edge vortex. Research on both real and model insects suggests that additional unsteady mechanisms come into play as the wing flips over and changes direction [11].

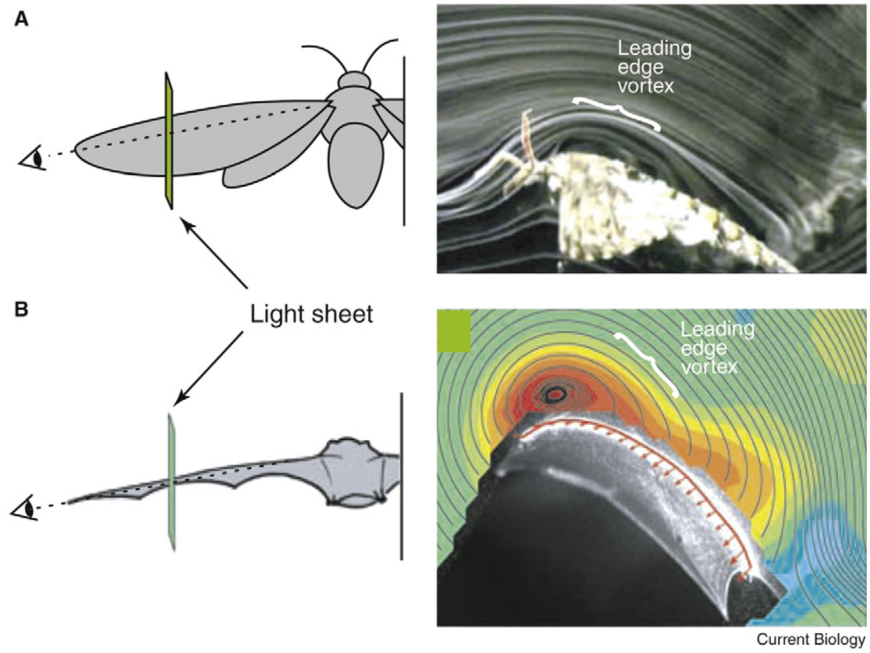

Figure 1. Moth wings and bat wings both make leading edge vortices.

(A) The wings of a large hawk moth create a prominent leading edge vortex during the downstroke, as visualized on a tethered animal flying in a smoke rake within a wind tunnel. The photograph shows the flow around a thin section of the wing (modified from [19] with permission of the Company of Biologists). (B) Bat wings, operating at the same Reynolds number (*Re* $\sim$ 5000), also create a leading edge vortex, as visualized using the technique of digital particle image velocimetry (modified with permission from [4], with permission from AAAS).

As complicated as insect aerodynamics may be, understanding bat flight promises to be even more challenging. Bats fly with large web-filled hands, which are capable of active shape changes throughout the stroke [13]. Just determining the complex motion of the wings throughout the stroke is difficult enough, and measuring the air flow around the wing would seem an impossible task. For these reasons, the recent paper by Muijres and colleagues [4] is an experimental triumph. Using a wind tunnel in Lund Sweden designed specifically for studies of animal flight, the research team was able to quantify the pattern of air flow around the wings of long-tongued bats flapping in front of a stationary feeder. Using a technique called digital particle image velocimetry [14], they were able to capture images of the flow field around the bat's wing. The results unambiguously show a leading edge vortex, stably attached to the wing during the downstroke. By quantifying the strength of the vortex, the authors estimated that the leading edge vortex accounts for about 40% of the lift throughout the stroke. Because of an important conservation law, the wake behind a flapping wing contains a trailing vortex with equal and opposite strength to all the vorticity created by a wing [15]. From their quantification of the strength of the trailing vortex, the researchers suggest that, like some insects, hovering bats use additional unsteady mechanisms during stroke reversal. This work compliments previous studies that suggest hovering hummingbirds [16] and fast gliding swifts [17] also create stable leading edge vortices. Although we will never know for sure about pterosaurs, all evidence would suggest that at least some members of all four flying taxa make or made use of leading edge vortices while hovering.

Are these new results surprising? In an odd but informative coincidence, both hovering bats and hawk moths operate at almost exactly the same *Re* ($\sim$5000). This means that, despite their size and taxonomic difference, the aerodynamics of the two animals should be similar, provided the pattern of wing motion is the same.

Unfortunately, the new paper [4] does not provide data on wing kinematics, but it is reasonable to think that the wing motion of hovering bats and moths is similar. Indeed, the new images of the bat wing and its leading edge vortex are uncannily similar to images captured previously for moths (Figure 1) [18,19]. As elegantly described by the great neuroethologist Ken Roeder [20], bats and moths are engaged in a deadly evolutionary arms race for command of the night sky. It is intriguing to note that these creatures are nevertheless united by the laws of physics.

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Cell Shape: Taking the Heat

Preservation of cell architecture under physically stressful conditions is a basic requirement for many biological processes and is critical for mechanosensory systems built to translate subtle changes in cell shape into changes in organism behaviour. A new study reveals how an extracellular protein — Spam — helps mechanosensory organs in the fruit fly to withstand the effects of the water loss that accompanies heat shock.

Patricia Kunda, Jennifer L. Rohn and Buzz Baum

Sensory systems allow animals to detect minute changes in their environment, including those accompanying adverse conditions. This information can then be used to induce an appropriate response, for example to guide the direction of movement or the selection of an adequate place to lay eggs. But some potentially harmful environmental changes, such as the daily fluctuations in ambient temperature, cannot be easily avoided; instead, they must be tolerated. This problem is likely to be particularly acute for sensory systems themselves, as they have evolved to be optimised for sensitivity to environmental changes.

Exposing a small animal such as a fruit fly to a simple heat shock will compromise the ability of its sensory systems to function by altering body temperature and the rates of many of the biochemical events involved in signalling. In addition, dry heat can induce a loss of water, resulting in osmotic shock. As mechanosensory organs are constructed to translate mechanical events at the cellular level into changes in organismal behaviour, this latter problem is likely to be especially acute. Under normal conditions, the movement of a bristle on the back of the fly will induce changes in the lipid bilayer and the underlying cortical cytoskeleton of mechanosensitive neurons, altering the regulated flow of ions across the plasma membrane through transient receptor potential (TRP) channels [1], in turn triggering an action potential that passes to the central ganglion to ultimately alter fly behaviour [2–4]. By disturbing the shape of the cells involved in mechanotransduction, osmotic shock is likely to compromise performance and to damage the delicate machinery involved in sensing bristle movement. Moreover, since TRP channels function in both mechanosensation and osmoregulation, osmotic shock may also induce aberrant signalling. How mechanosensory systems cope with such everyday environmental changes is therefore a pressing question in biology.

A recent paper from Charles Zuker and colleagues published in *Nature* sheds light on this problem [5]. By screening for changes in fruit fly behaviour, these authors identified a normally viable mutation in the gene *spacemaker (spam)* that sensitized flies to the effects of a 37°C heat shock. Whereas wild-type flies appeared unaffected by this treatment, mutant animals manifested severe and irreversible defects in their ability to walk, feed and fly. Intriguingly, Spam is a secreted protein containing several epidermal growth factor and laminin G-like repeats and was recently identified by the Zuker lab to be a structural component of the *Drosophila* eye [6]. In the eye, Spam