



Bats in the Air and on the Ground

Studying Locomotion and Muscular Design

From Horses to Bats

Studying the anatomy of four-legged mammals such as horses provides a fascinating window into the diversity of locomotion. I spend a lot of time at the College of Veterinary Medicine researching this. My colleagues and I have examined the spring-based locomotion of trotting horses, which is why horses can trot for great distances without depleting their energy reserves and why they have a nasty and uncomfortable bounce for novice riders at trotting speeds. Locomotion and muscular design are focal areas of my research. Model animals range from mouse to sheep to horse. So how do bats fit into this scheme?

Bat Locomotion

Bats are athletic mammals that are efficient flyers. They cover great distances quickly and efficiently. Having both ground and air locomotion, they offer fascinating prospects for answering all sorts of questions, and they are wonderful model organisms for training students. I was first intrigued by bats as an undergraduate. Subsequently, my early research focused on the anatomy and physiology of the muscles that power flight.

Working with two Cornell doctoral students, we recently focused on the other end of the bat—the hind limbs and how they contribute to a bat’s lifestyle. William Schutt, Ph.D. ’95, now a professor at Long Island University, studied the mechanism in the toes of bats that allows them to hang for long periods of time by the toes, without burning excessive energy. Just image yourself trying to hang from a branch for several hours—you could not. Schutt discovered an adhesive-like mechanism that held the toes in place for hours without the need to use muscular energy.

Several years later, Daniel Riskin, Ph.D. ’06, came from Canada where he had studied the ability of certain bats to “grasp” a smooth vertical substrate, like a glass surface. One of his bats, a species called *Thyroptera discolor*, had suction cups on the surface of its hands to allow such movement. These bats can walk up a vertical pane of glass. Riskin switched his attention at Cornell to biomechanics, particularly as applied to bat walking. Using force platforms, we assessed side-to-side, vertical, and forward accelerative forces in walking bats. Using the treadmill, we documented the gait transitions as bats went from walking to running gaits.

Bat Fascination

Bats have always been a great fascination for scientists. The vampire bat, for example, is like a mammalian version of a mosquito, with its unique mode of feeding on blood. These factors alone present many implications. Scientists have enormous interest in vampire bats because of their potential to spread rabies to humans and domestic species. But there are also numerous potential applications of bat research in human medicine and agriculture. Scientists have found, for example, that *bats*' saliva contains

to see more of the vampire's locomotor repertoire. The force platform provided exquisite data for several step cycles or strides at low speeds, but then the bats quickly moved off the platform and left questions to be answered. So we returned to Trinidad in 2003, armed with a treadmill sized just right for a 30-gram mammal, force platforms, and a new list of questions. The vampire bats were surprisingly tractable in our hands, and within minutes, they were walking while our recording system stored the data. We asked the bats to move increasingly

paralleled the gait transitions used by walking or running dogs and horses. For example, as a horse increases speed, it switches to different gaits—going from a walk to a trot to a gallop, with speed. These gait shifts allow speed to increase, while stride frequency (the rate at which a single limb proceeds from the start of the stance phase with the foot on the ground, through the swing phase, until the foot is again placed on the ground for the next step) decreases to a value lower than predicted for high-speed walking. Stride frequency has been correlated with the energetic cost of forward movement.

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an anticoagulant, and a pharmaceutical spin-off of this has resulted in an enzymatic protocol for busting blood clots associated with heart attacks in humans.

Cornell has a history of bat biology, going back to the published works of Burt Wilder, one of the first professors of comparative anatomy at Cornell. More recently, William Wimsatt, who held joint appointments in Genetics and Development and Physiology, trained numerous graduate and undergraduate students in bat biology.

Our Fascination

In 2003, Riskin and I returned to Trinidad to fine-tune our previously collected data about the ground-based locomotion of vampire bats. What we observed was far more than we expected. We had worked on these bats during the summer of 2002, collaborating with local wildlife biologists to identify hot spots for vampire activity. We located farmers whose cattle were being bitten nightly by vampires. To catch the vampire bats, we used special nets that we placed in an array around cattle in the nighttime pastures.

During the 2002 field season, the bats had walked on a specially designed array of two-force platforms that recorded the forces generated as the bats walked across a horizontal surface. Upon returning to Ithaca from this fieldwork, we knew that we needed

faster, and they were soon doing a comfortable but much faster walk than we anticipated. As the treadmill whirred by, the bats suddenly changed gaits and moved into some sort of bound or run.

Bats are supposed to fly, and fly well they do. There are over 1,000 species of bats, and only a handful are known to move effectively on the ground. Most are clumsy. Their long and slender wings and the manner of attachment of the wing between the forelimbs and hind limbs often make bats' walking comparable to a person trying to walk fast with a long, tight skirt.

Vampire bats "reinvented" walking and running gaits. If one considers the ancestors of vampire bats, none appeared capable of a walking gait, let alone a running gait. The early bats gave up their ground-based abilities in favor of some form of specialized flight. Some groups of bats are fast fliers, while others are slow but highly maneuverable. We were able to show that most comparable bats related to the vampires were clumsy while walking, and none were capable of high-speed movement on the ground. We recorded and quantified sequences of the common vampire bat running at about one meter per second for sustained periods of time.

Analysis of the vampire bat's limb movements revealed several interesting trends that

The common vampire bat is able to maintain low stride frequency at walking speeds and at high running speeds, which can rise to above two meters per second. We also found that the stride frequencies during walking were predicted by body mass, and therefore could be directly compared to mammals of similar size. Because of their very long forelimbs compared to other mammals, the common vampire bats had a relatively low stride frequency while running relative to a mouse or some other small mammal.

Keeping Pace with Prey

The common vampire bats that we studied feed on cattle in developed areas. They walk capably, almost as comfortably as any terrestrial mammal. They often approach their prey by landing nearby and walking up to the animal. Except for isolated reports of vampires feeding on humans in Brazil and one published report of vampires chasing terrestrial rodents, the modern vampires seem to feed exclusively on domestic cattle. Prior to the introduction of domestic livestock in South America, wild vampires probably fed on South American forest mammals, such as agouti and capybara, which are agile and quick. Most likely, it was necessary for the vampires to develop a mode of locomotion on the ground that would allow them to keep pace with a wary and highly mobile blood reservoir.

We also studied the closely related white-winged vampire bats (*Diaemus youngi*) in Trinidad. These bats specialize in feeding on bird blood and have moved into feeding on domestic fowl in agricultural situations in Trinidad. White-winged vampires are beautiful bats with large, childlike eyes. They are capable of walking on the ground and are



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stealthy climbers when pursuing chickens into nocturnal roosts in trees or raised nests around farms, but we never found the white-winged version of the vampire breaking into a running gait. Both vampires that we studied—there is a third species on the mainland of South America—fly well, but they are not the most adept or maneuverable of bats in flight.

Trinidad: A Place for Research and Outreach

Culturally and biologically, the nation of Trinidad and Tobago is quite distinct from Ithaca. It provides a useful window into the tropical world of bats and many other animals. Trinidad, a lovely, unindustrialized island, is a short hop from the South American mainland. The seven-mile water gap between Trinidad and Venezuela poses little challenge to the migration of vampires. We exchanged ideas with the “rabies men,” field biologists in the wildlife division of the government of Trinidad and Tobago, who are charged with controlling the ever-present threat of rabies passing from bats to humans or to domestic livestock. One of the last great outbreaks of human rabies occurred in Trinidad about 70 years ago. To this end, we gave seminars and conducted workshops with the local biologists. We also benefited immensely from our interactions with our hosts at the University of the West Indies.

Understanding the biological role of vampire bats is critical to the balance between controlling rabies and maintaining viable populations of the two vampire species that make their home in Trinidad. Local extermination efforts often put other species of bats at risk. Having informed biologists in the field assessing vampire populations and movements is critical to maintaining a healthy ecosystem. We have sporadically studied bat populations in several sites in Trinidad since 1990. Our field notes provide insight into the stability—and, in some cases, decline—of the many (about 65) non-vampire bat species found in these sites and more generally around the entire island.

More Vampire Bat Facts

Vampire bats are smart. They make eye contact with you. After one or two trials on the treadmill, they quickly learned the game. As soon as Riskin moved toward the on-off switch, they turned to face the front of the treadmill and started walking. I have seen

lots of cats on treadmills, and the word “cooperation” does not come to mind. Vampires have been shown to live in tightly organized family units, sharing blood meals with related bats that have not found food in a nightly flight. Vampire bats are derived from a South American family of bats (*Phyllostomidae*) that are known for a diversity of feeding styles, including insectivory, frugivory (fruit eating), and nectarivory. Many of these bats are important seed dispersers and pollinators, making their implications in agriculture and floral conservation significant.

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From My Bat Lab

Gerald Carter '05, a presidential research scholar, worked on the Trinidad project with Riskin and me for two years. He is now pursuing graduate study. Claudia Coen, Ph.D. '02, also worked with vampire bats on our Ithaca campus and in South America during several years of challenging field work. She examined the nutritional requirements of two of the vampire species (mammal blood versus bird blood), and now she has developed valuable programs for zoos that are interested in maintaining captive populations of all three vampire species. Coen continues to contribute to programs that enable public school teachers to educate their students about bat biology and bat myths.

What's Next in Our Bat Research?

In 2007 Dan Riskin and I will work together again in New Zealand in a collaboration with Stuart Parsons of the University of Auckland. Following up with our earlier studies, we plan to correlate echolocation pulses (the radar-like system that bats use to examine their world) with locomotory activity. For example, Are the bats vocalizing during specific phases of each wingbeat during flight? In the case of the New Zealand short-tailed bat, are they echolocating while walking on the ground or in burrows in search of prey?

In an ongoing study with Cornelia Farnum, Biomedical Sciences, we have integrated my work in field sites around central New York with her interest in the mammalian growth plate. Bats have enlarged fingers—the digital bones that underlie the wing. Farnum and I have investigated the remarkably rapid development of bone during the postnatal period in big brown bats. We hope to publish these results soon. This work is timely since other research groups have recently examined some of the molecular mechanisms that seem to coordinate growth and elongation

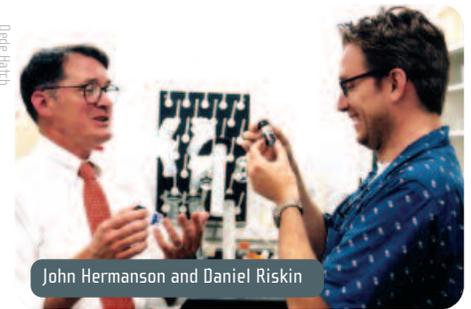
of mammalian bones. In particular, several published studies have noted the unique nature of bat wing bones.

Bats are an enormously important living group of mammals. It is energizing to be part of this collective research effort.

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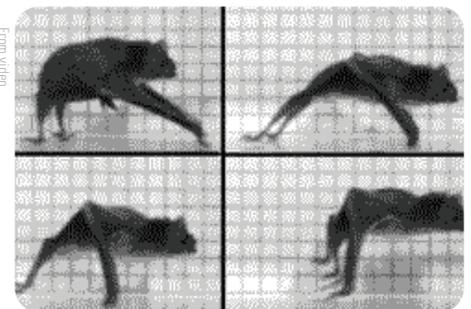
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Derek Heath



John Hermanson and Daniel Riskin

From video



FASCINATING



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