Bird class people: See the article ("Migrants Since Thoreau"), p. 26.

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Hummingbird Aerodynamics

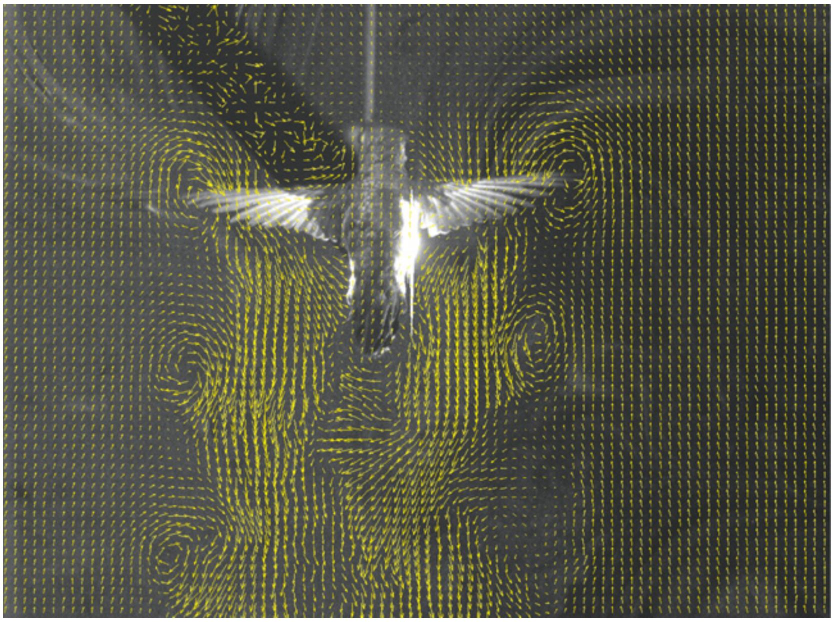
How does a hummingbird hover for so long with such seemingly little effort? After two years of experimentation with a primitive wind tunnel and a movie camera shooting 1,500 frames per second, Crawford Greenewalt took a famous first step toward an answer in his 1960 book, *Hummingbirds* (Doubleday). His pioneering frame-by-frame sequences stop the whirring wings and allow us to see what would otherwise be invisible.

Greenewalt interpreted the wings' movements as primarily forward and backward, "rowing" the bird through the air, rather than flapping. He saw, too, that the wing twists nearly 180 degrees on its long axis during the cycle. But he was stumped about aerodynamic cause and effect: "The resulting complexity of motion simply does not lend itself to detailed analysis. Perhaps with modern electronic computers something might be done, but until that very great effort is made, we shall have to rest content with our imperfect and rudimentary knowledge."

A half-century later, the aerodynamic details Greenewalt desired are becoming clear, thanks in part to intensive research at the University of Montana Flight Laboratory at Fort Missoula. Laboratory Director Bret W. Tobalske explains in a 2010 review what is currently known about factors that enable hummingbirds to hover <tinyurl.com/46kyfhp>.

The capability rests on a unique and exquisitely co-adapted combination of anatomy, physiology, and aerodynamics. Hovering in still air requires extremely high power from the flight muscles, and the primary muscles used for the downstroke and the upstroke are proportionally larger in hummingbirds than in other bird species. But size alone is not nearly enough. The flight muscles also have physical characters designed to make maximum use of the birds' high-energy metabolism. Further, the wings' skeletal design differs from that of most birds in features that may be adaptive for hovering.

Finally, there are aerodynamic considerations, which have posed the most puzzling questions. The Montana laboratory is producing answers with a high-tech method called particle image velocimetry, which displays patterns of air flow around the wings. Rufous Hummingbirds are trained to fly into a Plexiglass cube, where they hover at a feeder in which the field of air flow around the wings is illuminated by a laser. The air is seeded with minute particles of olive oil vapor, and the illuminated particles show the patterns of flow in detail. Simultaneous digital video photographed from above illustrates the wings' motion.



Science meets art in this photograph of a **Rufous Hummingbird** hovering in a wind tunnel at the University of Montana Flight Laboratory. The bright streaks illuminate patterns of air flow that help to make hummingbirds the foremost hoverers in the avian world. *Photo by © Bret Tobalske–University of Montana.*

Douglas R. Warrick, Tobalske, and Donald R. Powers describe the results of this method in a 2009 paper (*Proceedings of the Royal Society B: Biological Sciences* 276:3747–3752), available online <tinyurl.com/4pdztc7>. The aerodynamic details are arcane. Suffice it to say here that the process depends primarily on two aspects of air flow: a vortex along the wing's leading edge and a pattern of circulation across the wing's upper and lower surfaces.

Combined with the wing's rotation back and forth on its long axis—the "twist" that surprised Greenewalt—the air flow produces near-continuous lift during the entire downstroke and upstroke cycle. Unlike other birds' flight, there is no interruption in lift.

These and other significant findings are illustrated on the Montana Flight Laboratory's colorful website <tinyurl.com/4g7pktf>. The site includes video footage of birds in the wind tunnels, descriptions of past and current studies using various species, and many publications stemming from work at the laboratory.

Studies of hummingbird aerodynamics have enabled engineers to design a tiny unmanned aircraft modeled on hummingbirds' unique flight mechanisms. In February 2011, AeroVironment, Inc. demonstrated its creation of a remote-controlled "Nano Hummingbird" that can hover; fly sideways, forward, and backward; and rotate clockwise and counterclockwise. Check out online videos <tinyurl.com/4fxao4r> of the tiny robot's uncanny abilities, and read the story <tinyurl.com/4nmwjd3> behind this historic achievement.

Mercury Strikes Again

Is there no end to what we will learn about the toxic effects of mercury on birds? More than half a century of research has revealed a widening swath of damage across the entire *ABA Checklist*—that is, all the way from waterfowl to finches.

Every year, scientists add pages to a catalog of hormonal aberrations, reproductive defects, developmental abnormalities, and behavioral disorders. Each of those categories has its own assortment of deviations, including some—such as atypical songs—that may have potential effects on species' evolutionary future.

The strangest new discovery involves White Ibis breeding productivity. An experimental study links mercury to reduced nesting success and demonstrates an eyebrow-raising reason why many nests produce no young: Both members of the poisoned nesting pairs are males.

Peter Frederick and Nilmini Jayasena reported the findings online in 2010 in *Proceedings of the Royal Society B: Biological Sciences* <tinyurl.com/4ccnocl>. They captured 160 White Ibis nestlings from breeding colonies in southern Florida and raised them in a compartmented free-flight aviary. Three randomly separated groups (20 of each sex per group) were given food tainted with methylmercury in different dosages spanning the range of concentrations found in ibis prey in the Everglades. A fourth group, serving as an experimental control, received no dose.

Methylmercury is the toxic organic compound synthesized by microorganisms from inorganic mercury, which enters the environment mostly in coal-fired power plant emissions. The toxin passes upward through the food chain in larger concentrations until it reaches top-level predators such as the ibis.

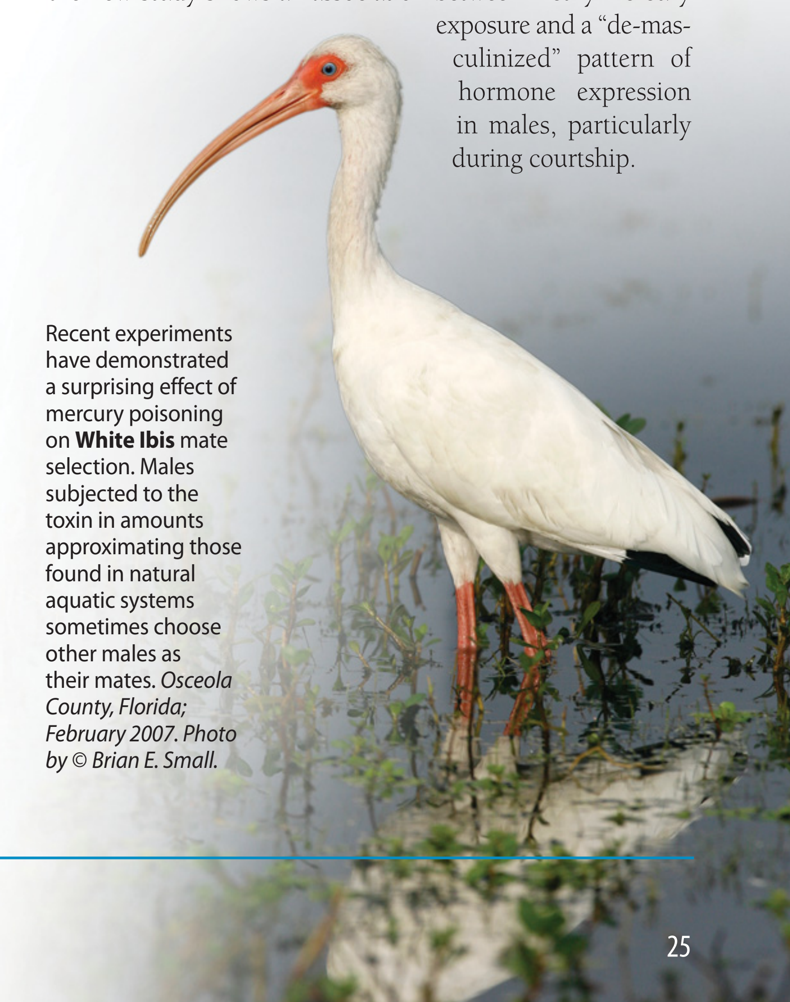
In three years of experiments, every dosed group had a greater proportion of nests without eggs than the control group. Depending on the dosage, the poisoned groups' overall loss in productivity ranged from 13% to 15% compared to the control group. More striking is what Frederick and Jayasena reported next: Varying with dosage, 74% to 91% of those complete nesting failures resulted from male–male pairings.

The study also revealed that heterosexual pairs' breeding success can be damaged by methylmercury. Overall in the study, dosed pairs produced an average of 35% fewer fledglings than the control pairs. The authors emphasize that damaging levels of exposure in the relatively low-dose groups were as low as levels found in many U.S. aquatic systems.

Those experiments were not undertaken in a vacuum of knowledge. Previously investigating White Ibis breeding activity in the Everglades, Julie A. Heath and Frederick had found correlations suggesting that methylmercury exposure may have caused fewer birds to nest and more birds to abandon nests.

However, Heath and Frederick reported in 2005 (*Auk* 122:255–267) that their results could not tease apart effects of the toxin and other possible environmental factors. They needed a controlled environment to establish causal relationships between reproductive success and the toxin alone, and the new experiments succeeded in isolating the effects.

Frederick and Jayasena say the physiological mechanism linking methylmercury with male–male pairing remains unknown. It may involve both behavioral and hormonal factors. Sexual display in birds is influenced by hormone levels, and the new study shows an association between methylmercury exposure and a "de-masculinized" pattern of hormone expression in males, particularly during courtship.



Recent experiments have demonstrated a surprising effect of mercury poisoning on **White Ibis** mate selection. Males subjected to the toxin in amounts approximating those found in natural aquatic systems sometimes choose other males as their mates. *Osceola County, Florida; February 2007. Photo by © Brian E. Small.*

Whatever the pathway, this is the first time methylmercury has been shown to influence birds' sexual preference. Now the question is whether other species are similarly affected.

Migration Since Thoreau

"I am on the alert for the first signs of spring, to hear the chance note of some arriving bird." That is Henry David Thoreau in *Walden*, and his vigilance produced a treasure of birds' arrival dates at Concord, Massachusetts, from 1851 to 1854.

During approximately the same period, he recorded plants' first flowering dates, and in his journal in 1852 he suggested an ecological link between plants' and birds' phenologies: Insect abundance tracks the timing of vegetation, and birds track the timing of insect abundance. Thoreau's insight was that if buds emerge too early and are killed by frost, insect abundance will fall, and the birds will suffer.

How gratified he would surely be to learn that biologists a century and a half later are finding ecological importance in his records. Further, how concerned he would surely be to know that the timing has slipped out of synchrony. Two recent papers document the divergence.

Abraham J. Miller-Rushing and Richard B. Primack at Boston University describe vegetational timing in a 2008 paper (*Ecology* 89:332–341). Plants of 43 species were flowering an average of seven days earlier at Concord during 2004–2006 than Thoreau had recorded for those species in 1852–1858.

Correspondingly, the average annual temperature at Concord warmed 2.4° C from 1852 through 2006. Miller-Rushing and Primack associate this rise with both global climate change and a local "heat-island" effect in the increasingly urbanized Concord area. Flowering times were most strongly correlated with temperatures in January and in the one or two months just before flowering.

Elizabeth R. Ellwood, Primack, and Michele L. Talmadge wondered whether spring migrants were arriving earlier at Concord in concert with earlier flowering. They reported in 2010 that the overall answer is no (*Condor* 112:754–762). The authors compared dates for 22 species that appear both in Thoreau's 1851–1854 data and in 1988–2007 records kept by retired teacher Rosita Corey in Concord. Averaged across all 22 species, there was no change in arrival date.

Among the 22 species, the picture varied. Three arrived earlier during 1988–2007: Warbling Vireo, Yellow Warbler, and Baltimore Oriole. Four arrived later: Bank Swallow, Barn Swallow, Wood Thrush, and Ovenbird. Fifteen were unchanged: Eastern Wood-Pewee, Eastern Phoebe, Eastern Kingbird, Red-eyed Vireo, Gray Catbird, Brown Thrasher, Yellow-rumped Warbler, Pine Warbler, Black-and-white Warbler, Common Yellowthroat, Chipping Sparrow, Scarlet Tanager, Rose-breasted Grosbeak, Indigo Bunting, and Bobolink.

An annual climate-related correlation did appear when Ellwood and her colleagues inserted arrival data from intermediate periods recorded by William Brewster in 1886 and 1900–

The Walden woods, immortalized by Henry David Thoreau a century and a half ago, are adding a new chapter to their iconic legacy. Birds' spring arrival dates meticulously recorded there by Thoreau are being compared to the same species' arrival timing today. *Concord, Massachusetts. Photo by © Matthew R. Burne–Walden Woods Project.*

1919, by Ludlow Griscom in 1930–1931 and 1933–1954, and by Corey in 1956–1973.

Overall, the 22 species averaged earlier arrival in years of relatively warm March and April temperatures. Again, the picture varied. Eastern Phoebe, Warbling Vireo, Yellow Warbler, Yellow-rumped Warbler, Chipping Sparrow, Scarlet Tanager, and Rose-breasted Grosbeak arrived earlier in warmer springs. Wood Thrush actually arrived later. The others' arrivals were not correlated with March–April temperatures.

Beneath the varying particulars is a general long-term disconnect between earlier flowering and unchanging arrival of migrants—but for now, Ellwood, Primack, and Talmadge consider their findings preliminary. Before assessing possible ecological effects on migrants, they need what they call "the missing link": data on emergence of insects in relation to temperature at Concord. Then Thoreau's hypothesis about weather, insect abundance, and birds could be fully tested.

Vireo Breeding Discoveries

Behavioral variations within a species are often more interesting than variations among species. Female breeding behavior in a Blue-headed Vireo population in Pennsylvania offers an intriguing example. Unlike behavior noted elsewhere, this population's females desert their nests on or near the day the young fledge, leaving care of fledglings to the males.

Eugene S. Morton, Bridget J. M. Stutchbury, and Ioana Chiver reported the females' activity in 2010 as the first example in passerines of consistent brood desertion by one sex (*Behavioral Ecology and Sociobiology* 64:947–954).

Morton and several colleagues first saw signs of the behavior while they were studying vireo nestlings in 1994 for other research. They were surprised that five females deserted their broods before nestlings were at fledging age.

During 12 subsequent years, Morton, Stutchbury, and Chiver documented female desertion in all 24 successful nests they could observe at the fledging stage. Of six females radiotracked near the fledging period in 2008, one deserted as early as three days before the young fledged, and the others departed on the day of fledging. No males were detected deserting, and the males alone cared for the young.

Females in a **Blue-headed Vireo** population in Pennsylvania show an aspect of breeding behavior that has not been documented in this species elsewhere. These females desert their nest on or near the day the young fledge, leaving care of the fledglings entirely to the male. *Allegheny County, Pennsylvania; October 2010. Photo by © Steve Gosser.*

Radiotracking produced a second discovery: From one to four days before their young fledged, the females made forays as far as two kilometers to check out prospective new mates. After desertion, six of these females averaged less than five days before they laid their first egg in a new nest with a new mate on a new territory. In contrast, males averaged 20 days after their brood fledged until a new mate laid an egg in the new nest.

Females deserted only successful nests. When the nest was lost to predation, they remained to renest quickly with the same mate.

Morton, Stutchbury, and Chiver discuss various possible paths of natural and sexual selection that might promote desertion. For example, if a female departs at the point when her mate can successfully care for her young, renesting more quickly with a new mate would enhance her productivity. The authors also speculate that this behavior would most likely occur in a population where males outnumber females, and the female could find a new mate relatively easily.

Is female desertion unique to the population in northwestern Pennsylvania? Naturalist Aretas A. Saunders, working in Allegany State Park in western New York, reported different behavior. "When the young are out of the nest, parents are still busy feeding them for a few days," he wrote in 1938 (*New York State Museum Bulletin* No. 318).

In his *Birds of North America Online* species account <tinyurl.com/4qq83ho>, Ross D. James reports another pattern of parental care in Ontario in which the parents feed young for at least a few days and "soon split apart, each taking some young and going separate ways." James tells *Birding* that he has not seen female abandonment in Ontario or indications of a second brood except when a pair renests after its first nest was destroyed. About possible differences in the breeding behavior, he says, "Many things could be found out, but it often takes much time and dedication to be certain."

Morton, Stutchbury, and Chiver emphasize that further study of individually recognizable birds is needed to learn whether female desertion differs among Blue-headed Vireo populations, whether it occurs in other vireo species, and whether it exists in other songbird families.