



"Monarch whispering", Mexico, December 2006. (Photo © L.P. Brower)

Lincoln Brower's European Tour

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Lincoln Brower has been studying the North American monarch butterfly, *Danaus plexippus*, for more than 50 years, and for 30 years he has made preservation of the unique migration of this butterfly a personal mission. To honour his research and conservation efforts and to celebrate his 75th birthday, this summer Lincoln was invited to participate in a series of events in London and Italy. On 27 June, Lincoln presented the 2007 Frederick W. Edwards Lecture in Insect Natural History at London's Natural History Museum, South Kensington. The following afternoon Lincoln addressed a joint meeting of the Royal Entomological Society and the Linnean Society of London, held at the senior society's rooms at Burlington House, Piccadilly, and was also presented with the 2007 Marsh Award for Insect Conservation by Brian Marsh, on behalf of the Marsh Christian Trust and the RES. After

these London events, Lincoln was feted in Italy with a symposium in his honour as part of the Fifth International Conference on the Biology of Butterflies, held at the famous Villa Mondragone Congress Center, Monte Porzio Catone, near Rome. Lincoln's European Tour was generously sponsored by the British Ecological Society, the Royal Entomological Society, the Linnean Society of London, and the Department of Entomology of the Natural History Museum.

Biography of Lincoln P. Brower

As a contribution to the symposium held at Villa Mondragone, *LSF* gave a biographical account of Lincoln and his work, on which the following narrative is based.

Lincoln Brower was born in New Jersey in 1931. An interest in butterflies arose early and was



Trinidad 1963 – left to right, Lincoln Brower, Jane Van Zandt Brower and Gary Stiles, at the William Beebe Tropical Research Station. (Photo © L.P. Brower)

encouraged by his mother and two aunts, one of whom introduced him to an immigrant German entomologist named Charles Rummel. Rummel, along with other Germans who were the core of the Newark (N.J.) Entomological Club, included Lincoln on collecting expeditions, and taught him to inflate hawkmoth caterpillars and to sugar for *Catocala* moths. By the time Lincoln headed to Princeton University as an undergraduate, he wanted to study butterflies. By this time, too, his high school classmate Jane Van Zandt was a frequent field partner. Lincoln and Jane married and together entered the Ph.D. program in Zoology at Yale University. With Charles Remington as their major advisor, Lincoln addressed speciation in the *Papilio glaucus* group, and Jane carried out the first controlled experimental test of Batesian mimicry in butterflies.

Lincoln subsequently accepted a faculty position at Amherst College, a small liberal arts college in Massachusetts. For the next 22 years he ran a tremendously productive research programme, making major contributions to the fields of mimicry, butterfly courtship, chemical ecology, predator behavior and prey defense (see bibliography). Lincoln had a gift for mentoring undergraduate students in research, and he included them as co-authors on many publications. Among biologists who were introduced to research in Lincoln's lab are insect behavioral ecologist John Alcock, *Drosophila* biologist John Jaenike, and tropical ornithologist Gary Stiles. In the 1960s summer research was conducted first at the Archbold Biological Station in Florida, and then at the William

Beebe Tropical Research Station (Simla) in Trinidad.

While on sabbatical at E.B. Ford's lab in Oxford during 1963–64, Lincoln and Jane reviewed the evidence that unpalatable butterflies acquired protection by sequestering toxic chemicals from their larval hostplants (Brower and Brower 1964). They reasoned that if butterflies gained chemical protection from hostplants, then raising caterpillars on nontoxic hosts would produce palatable adult butterflies. Back at Amherst, over several generations of selection they succeeded in raising a stock of monarch butterflies on cabbage rather than on milkweeds. Experiments with blue jays demonstrated that the cabbage-fed butterflies were not toxic (Brower, Brower and Corvino 1967). The Amherst lab shifted its focus from mimicry to the ecological chemistry of the interactions among milkweeds, monarch butterflies and bird predators. An organic chemist at Mount Holyoke College, Kenneth Williamson, collaborated with Lincoln in developing a spectrophotometric assay that allowed quantification of the cardenolide content of individual butterflies. Lincoln's lab began measuring the cardenolide content of monarchs reared on different milkweed species. Through the 1970s they demonstrated that variation in butterfly palatability was derived from variation in cardenolide content, that butterfly cardenolides reflected the hostplant's cardenolides, and that monarch populations in the wild display a palatability spectrum (Brower et al. 1968, Brower 1969, Brower et al. 1972, Brower and Moffitt 1974, Brower et al. 1975).

In 1976 *National Geographic* magazine announced that the winter home of the eastern population of monarch butterflies had been found in Mexico. Lincoln teamed up with a postdoctoral associate at the University of Massachusetts, Bill Calvert, who located the wintering colonies. Since 1977 Lincoln has been immersed in studying the winter physiology, ecology and behavior of monarchs in Mexico; and in working to conserve the tiny winter enclaves against a barrage of human threats. In 1980 Lincoln moved from Amherst College to the Department of Zoology at the University of Florida, which gave him more time for research and allowed him to supervise graduate students. Retiring in 1997, he moved to Virginia, where he is now a Research Professor of Biology at Sweet Briar College.

At age 75, Lincoln continues to make several research trips to Mexico each winter, supported by a grant from the U.S. National Science Foundation. To reach the butterflies, he navigates kidney-jarring dirt roads and travels precipitous trails on horseback, and then hikes on steep slopes at 3000m elevation.

Lincoln's London Lectures

Lincoln Brower has strong ties to British entomology and has been a Fellow of the Royal Entomological Society since 1975. He spent two years in the ecological genetics lab of E.B. Ford at Oxford (1957–58 and 1963–64), and in 1981 he was a plenary speaker at the First International Conference on the Biology Of Butterflies, organized by the RES. In 1993 the Linnean Society of London awarded him the Linnean Medal for Zoology. With mimicry as a research interest, Lincoln has always had special regard for Alfred Russel Wallace and Henry Walter Bates. It was with great pleasure, therefore, that Lincoln came to London to talk about monarch butterfly biology and conservation.

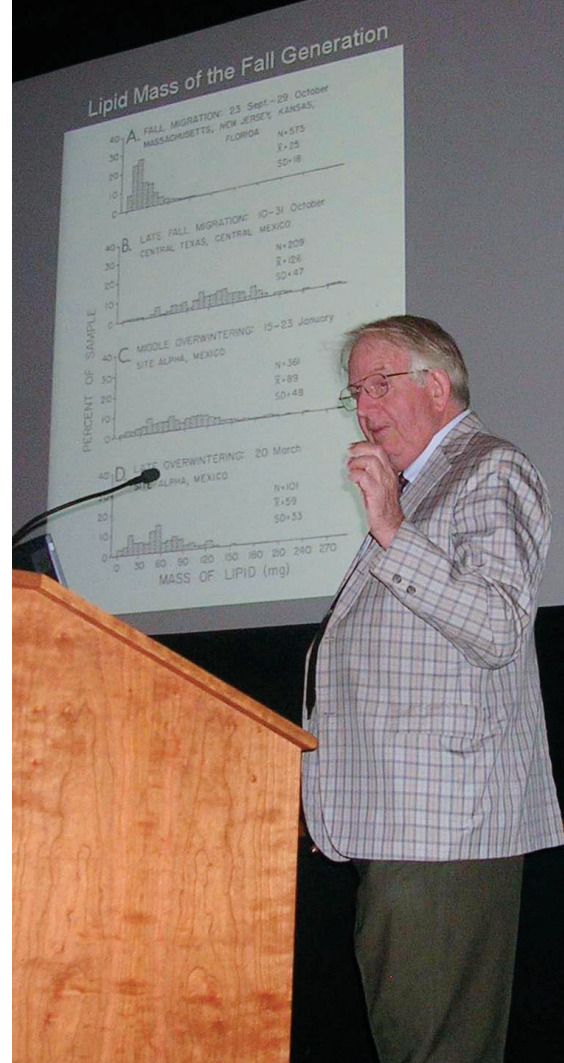
Lincoln's first lecture, at the Natural History Museum, "Conservation and Survival of the Migration of the Monarch Butterfly," began with a new seven minute video showing millions of monarch butterflies in Mexico roosting on fir trees, flying to water to drink, and mating. After introducing the beauty

and intricacy of the butterflies' migration, he outlined first the conservation challenges faced by monarchs during breeding and migrating in the United States and Canada, and then the challenges faced on the wintering grounds in Mexico. The major breeding areas overlap closely with the midwestern agricultural belt, and monarchs are losing breeding habitat as herbicides are used to convert vast agricultural swaths into GMO crop monocultures. Not only are milkweeds lost as larval hostplants, so are nectar sources that adults need to accumulate lipid reserves that form their vital winter energy source.

In Mexico, monarch butterflies are highly selective in their winter habitat, using very few hectares each year. Lincoln witnessed logging in the wintering areas during his earliest trips in the 1970s, and quickly became concerned about maintaining the forests' integrity. Clear cuts destroy forest habitat, and thinning alters the microclimate. As demonstrated by Lincoln and his students, thinning increases butterfly mortality during storms by exposing them to lower night temperatures and increased wetting. Having advocated strong protection for the wintering sites, and working in collaboration with Mexican environmental activists, scientists and NGOs, Lincoln pressured successive Mexican presidents to sign protective decrees, which they did in 1980, 1986 and 2000. Today, more than 56,000 hectares have complete or partial legal protection from logging. Recent photographs, however, show that logging is continuing within theoretically protected areas. The unique land tenure system in Mexico, established after the Mexican revolution, is a hindrance to forest conservation. Land is owned and governed by communities, called ejidos, and the federal government has little authority to enforce its mandates. Many ejidos resent the federal government dictating how they use their land. Other ejidos are trying to protect their forests, but without help from the government they are unable to evict illegal loggers. In addition to logging, other threats to the forests include soil erosion and the wholesale diversion of water that is essential to monarchs for drinking.

Despite these problems, Lincoln expressed cautious optimism. Funds are available to pay ejidos not to cut trees, and several ejidos are successfully managing their forests. Local conservation groups are providing education in sustainability, and are planting large numbers of trees in reforestation efforts. We must hope that these efforts will succeed. For three winters Lincoln and his postdoctoral associate Dan Slayback have used small planes for aerial reconnaissance of the entire region of Mexico where the butterflies winter. They did not find any wintering colonies other than those already known from ground reconnaissance. Their finding confirms that the small, unbelievably dense colonies of butterflies that blanket trees and fill the skies with orange are a rare, endangered biological phenomenon.

At the Linnean Society of London, Lincoln lectured on "King of the New World: the Adaptive Repertory of the Monarch Butterfly." With evolutionary biology under frequent attack by creationists and conservative politicians in the U.S., Lincoln was honoured to be lecturing in view of portraits of Charles Darwin and Alfred Russel Wallace. In an historical review of his fifty years of monarch research, he showed how each discovery led to more questions, and how he sought colleagues and new techniques that allowed him to address them. Lincoln pointed out that chance and luck had also played a part in his research. If he had reared monarchs on *Asclepias tuberosa* rather than *Asclepias curassavica* in early palatability experiments, the butterflies would not have been emetic to blue jays, and his work on sequestration and palatability might have stalled or been abandoned. If Lincoln's research team had not been camping at a butterfly site in Mexico in January 1981 when a severe snow storm killed a substantial fraction of the butterfly population, it might have been many years before he grasped the importance of the forest's microclimate for butterfly survival and conservation. Lincoln shows unabated enthusiasm for his butterflies. Although the majority of his research since 1966 has been on just one species, the questions he has addressed range from behavior, ecology and evolution to chemistry, physiology, climatology and



In full flow, Lincoln giving the Edwards Lecture for 2007 in the NHM's Flett Theatre, 27th June 2007.

(Photo by R.I. Vane-Wright)

geography. After fifty years he continues to raise important questions about the monarch butterfly, and he shows no signs of waiting for someone else to answer them for him.

Biology of Butterflies Symposium

The 5th International Conference on the Biology of Butterflies took place at Villa Mondragone, 2-7 July 2007, under the direction of Professor Valerio Sbordoni of Tor Vergata University, Rome. With over 250 contributing authors, 11 symposia, a student session and 40 posters, the whole conference was a tribute to the vigour of academic interest in butterfly biology, the genius of Valerio and his team of organizers, and the stamina of the delegates — who, not content with hearing about butterflies all day long, could be found debating the issues into the night in cafés and bars throughout Monte Porzio Catone and Frascati.

The opening session, on the afternoon of 2nd July, was the *Symposium in Honour of Lincoln*



Lincoln with reserve guides at a monarch overwintering site, Mexico. (Photo © L.P. Brower)

Pierson Brower. The programme of eight papers was organized by Karen Oberhauser (University of Minnesota), Michael Boppré (University of Freiburg) and Dick Vane-Wright. The first five presentations reported current research addressing major issues that Lincoln Brower's monarch work has done so much to stimulate: monitoring programmes for developmental stages and adult movements in North America (Karen Oberhauser), differential susceptibility to parasitism of different subpopulations undergoing seasonal migration (Sonia Altizer, Elizabeth Lindsay and Jacobus de Roode, University of Georgia), variations in the size of overwintering populations in Mexico in relation to climatic fluctuations (Chip Taylor, University of Kansas), survival and growth of larvae from different populations on local and alien milkweed hosts (Stephen Malcolm, Western Michigan University, and Myron Zalucki, University of Queensland), and sequestration of secondary plant chemicals by larval and adult *Danaini* (Michael Boppré).

The last three papers took a more historical approach. Dick Vane-Wright suggested that the breadth of Lincoln's contributions to monarch biology could be appreciated by seeing them in light of systems theory and 'ecological literacy'—underling that the monarch is a real icon for understanding how the living things on which we all depend exist, thrive and evolve as part of the biosphere. Linda Fink, in the unlucky absence of her co-author Andrew Van Zandt Brower, delivered the omniscient biographical account summarized above. Finally, the master himself delivered a brilliant grand synthesis of his two London lectures, and more, under the title "A half century journey with the monarch butterfly." The session closed with the presentation to Lincoln, made by Valerio Sbordoni, of a special medal commemorating the occasion, followed by a delightful reception, the "Lincoln Pierson Brower celebration."

Acknowledgements

As Lincoln's wife and research colleague, *LSF* would like to thank all

individuals and societies who hosted our European Tour. We will long remember the warm hospitality, including spirited conversations over tea, beer, and dinners; a walk through the Kent countryside; and the careful attention paid to the details of our travel, lodgings and lectures. Fifty years is a long history, and the lectures provided a welcome excuse for both Lincoln and me to review his early papers and ferret through his great archive of photographs. *RIVW* would like to thank the four sponsoring societies, together with Gretchen Bauta, for their ready and willing support of the lecture tour; staff and colleagues at the NHM and Linnean Society for staging the London presentations; co-organizers Karen Oberhauser and Michael Boppré and our speakers for making the Brower symposium such a success; and Valerio Sbordoni and his team from the Department of Biology, Tor Vergata University, and *ReS servizi Sas*, for organizing a wonderful conference. Finally, I wish to thank Lincoln and Linda for rising to the challenge, and being the stars in a truly memorable series of events.

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