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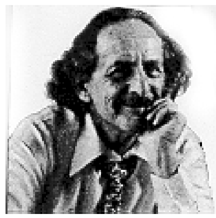

A Tribute to Miriam Rothschild: Entomologist *Extraordinaire*

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In a recent essay, I reviewed the latest publications of ISI Press®.[1] Among these is a biography of the turn-of-the-century British zoologist, Walter Rothschild, entitled *Dear Lord Rothschild: Birds, Butterflies and History*.[2] The book was written by Miriam Rothschild, a distinguished entomologist who is also Walter's niece. She has produced a most entertaining and informative account of his life and scientific achievements.

Dear Lord Rothschild has been well received by the scientific and lay press.[3-6] The book establishes beyond a doubt that significant contributions to zoological systematics, nomenclature, and microevolution were made at Tring Museum, which Walter Rothschild founded and administered for 50 years. Yet for all its value as science history, the book is leavened with entertaining insider's anecdotes about some of the most powerful people in Victorian and Edwardian England. And as the only book about a Rothschild written by a Rothschild, the work has special authority.

Meeting Miriam Rothschild prompted me to analyze, for the first time, the entomology journals indexed in *Science Citation Index*® (*SCI*®).[7] It also confirmed my feeling that the work of this remarkable scientist merited a thorough review. In this essay, I will discuss her most important research in several areas of entomology. I will also try to convey some sense of Rothschild the individual, for she is a dynamic and unconventional personality with a boundless range of interests.

Rothschild was born into the eminent Rothschild family on August 5, 1908. Her father, Charles Rothschild (Walter's brother), was an enthusiastic amateur zoologist. In free time snatched from the demands of the family business, he managed to publish over 150 scientific papers on fleas. He was also one of Tring Museum's major collectors.

For 27 years, Rothschild lived at Tring Park, Hertfordshire, northwest of London. Tring Park was the site of her uncle's natural history museum. This museum housed the largest collection of animal specimens assembled by one person. It contained more than two million butterflies and moths, 300,000 bird skins, 144 giant tortoises, and 200,000 birds' eggs. Given this environment and her father's influence, it's not surprising that the young Rothschild evinced a passionate attachment to insects, birds, and all other animals. She began breeding ladybirds when she was only four years old.

Like most women of her day, Rothschild was educated at home. In fact, the Rothschild family did not favor formal education for either sex. Her uncle endured only the minimum of university rote learning before breaking away to conduct independent zoological re-

Miriam Rothschild

searches. Similarly, her father had maintained that formal education stifled intellectual creativity.

Rothschild gleaned her education from her parents, her uncle's museum, and her own wide reading. Her own attitude toward formal education might be summed up by her statement, "The types of tests devised by the appropriate authorities in Britain today assess the size of the child's bottom rather than that of its head."[8] Although she did take courses at the University of London, she has never received a formal degree. Instead, she chose to work outside the educational system. The academic credentials Rothschild has acquired, such as the honorary doctor of science degree she received from the University of Oxford in 1968, she wrested from the educational establishment by the sheer compelling merit of her research. Her work also earned her the status of honorary fellow, St. Hugh's College, Oxford. Despite her lack of formal credentials, she served as visiting professor of biology at the Royal Free Hospital School of Medicine, London, from 1968 to 1973.

Lack of conventional education has in no way curbed Rothschild's research output. She has published over 275 works in fields ranging from marine biology to plant/insect interactions. As a child, Rothschild studied butterflies and ladybirds, but her zoological interests later crystallized around marine biology. Indeed, her earliest publications include a series of papers on the effects of flatworm parasites (trematodes) on a species of marine snail.[9-11] These papers showed that parasitism by larval trematodes causes abnormal growth in the marine snail. Trematode infestation also causes variations in shell development. These findings had important implications for snail taxonomy.

Rothschild inherited from her father an interest in fleas. Charles Rothschild had amassed at Tring Museum the largest collection of fleas in existence. He coauthored many papers with Karl Jordan, a curator of Tring Museum and a respected entomologist. Among these was a paper identifying the plague-carrying rat flea *Xenopsylla cheopis*.[12]

Initially, however, fleas were a sideline for Rothschild. Although she occasionally published descriptions of new species, she did not study fleas in depth until the 1950s. Then she began cataloging her father's flea collection. The first of the six-volume series covering the taxonomy and morphology of the collection was published in 1953. Rothschild coauthored five of these volumes with G. Harry Hopkins.[13] She has recently coauthored another work based on her father's collection.[14]

Around this time Rothschild also published jointly with Theresa Clay, formerly of the British Museum of Natural History, a popular work entitled *Fleas, Flukes & Cuckoos*.[15] This was part of a series intended to promote neglected facets of British natural history such as parasitology. In it Rothschild explained for the lay reader parasitism, symbiosis, and other species interrelationships. The book incorporated many of her interests, as it discussed fleas, protozoa, flatworms, flies, mites, microparasites, the fauna of birds' nests, skuas (gull-like seabirds), and European cuckoos. Clay contributed a chapter on feather lice.

Fleas, Flukes & Cuckoos proved that Rothschild could communicate science in a very palatable fashion. Characteristically, she served up the facts with a generous measure of levity. For example, she introduced her discussion of avian fleas by saying: "Birds' fleas and feather lice do not sing. Nor do they fly about flashing brilliantly coloured wings in the sunshine. It is scarcely surprising that in Britain bird and butterfly enthusiasts number thousands, but the collectors of fleas and lice can be counted on the fingers of one hand."[15] (p. 56)

But Rothschild's most important work on fleas was yet to come. In the early 1950s, the British Ministry of Agriculture formed a committee (which Rothschild was invited to join) to study the flea's role in transmitting myxomatosis, a viral disease of South American rabbits. The disease had reached England and was devastating the British rabbit population. To conduct the study, it was necessary to breed the rabbit flea in captivity. Other flea species bred readily in the laboratory, but the rabbit flea would not cooperate. Rothschild suggested that the host's hormone cycle might influence the flea's sexual maturation. This hunch was borne out when an associate demonstrated that the ovaries of the female rabbit flea matured only on pregnant rabbits.[16]

Rothschild then conducted a series of experiments to determine which hormones were at work. She and an associate, Bob Ford, showed that corticosteroids produced by the adrenal glands during late pregnancy, as well as estrogens, are the most influential hormones controlling ovarian maturation.[17,18] It was also found that in nature rabbit fleas copulate only on newborn rabbits, although they mature sexually on the pregnant doe. The fleas transfer from the mother to the newborns at parturition of the host. This ensures a food supply for the flea larvae, which feed on debris in the rabbit nest. Rothschild, Ford, and M. Hughes identified a pheromone, an airborne chemical stimulus produced by the newborn rabbits, that aids sexual maturation.[19] But they concluded that a simple change of host actually induces copulation of the sexually mature, egg-bearing fleas. The rabbit flea was the first known case of an insect parasite whose reproductive cycle is dependent on that of its host.[20]

Rothschild's flea studies included an elucidation of their jumping mechanism. In a series of articles published in the early 1970s, Rothschild and associates used high-speed photography combined with precise morphological studies to determine the exact jumping mechanism of *Xenopsylla cheopis*, the vector of plague.[21-23] Their findings suggest that fleas are descended from winged ancestors, since the jumping mechanism employs modified flight structures. These include the presence of resilin, a rubber-like protein, in the pleural arch of the flea's thorax.

Rothschild's flea research features prominently in the citation accompanying her honorary degree from Oxford.[24] The citation refers to her coming "to this our Capitol, not by degrees, but by one leap as of her fleas, in a triumphal chariot, so to speak, drawn not by Venus' doves, Juno's peacocks, Alexander's gryphons, Pompey's elephants, but by her sixty-odd species of avian parasites." The citation goes on to itemize her work on fleas, saying, "One flea (of the genus [sic] *irritans*) is enough for most of us, but she has faced some twenty-two thousand and despatched them."

Although Rothschild's work in ornithology is not as extensive as her work in fleas, to some extent these studies overlap. A number of her papers discuss bird fleas specifically.[25,26] In addition, she has studied the wood pigeon,[27] the black-headed gull,[28] and the mountain chough (a relative of the crow).[29] Perhaps her most arresting discovery was that wood pigeons with darkened plumage, which appeared in England in the winter months, were suffering from tuberculosis of the adrenal glands. Previously, they were thought seasonal migrants from another country. This discovery was economically important, because wood pigeons were a major source of avian tuberculosis among cattle. Unfortunately, Rothschild's discovery was made during World War II and wartime censorship prohibited publication of these findings.[30,31]

Rothschild never completely abandoned her childhood interest in butterflies. When she married in 1942 and began having children of her own, this interest was resurrected. After all, children are most easily introduced to natural history through these colorful creatures. Rothschild had four children and adopted two more. Her oldest son, Charles Lane, is now a biochemist. She credits him with inspiring, at the age of ten, many ideas for the new field of plant/insect interactions she pioneered through butterfly studies.[30]

One of Rothschild's major contributions to this field was her research on the defensive use by insects of toxic plant secondary substances. Secondary substances are plant products other than those necessary to sustain growth. Some of these substances are used in plant defense, but the function of many is unknown. Caffeine and digitalis are examples of plant secondary substances useful to humans.

According to *SCI* for the period 1955-1983, Rothschild's most-cited experimental paper in this field, cited 75 times, concerns heart poisons in the monarch butterfly.[32] This was published jointly with Tadeus Reichstein and Josef von Euw, both of the University of Basel, Switzerland, and J.A. Parsons, National Institute for Medical Research, London. Reichstein received the Nobel prize in physiology or medicine in 1950 for his work on the hormones of the adrenal cortex, including the isolation of cortisone.

This highly cited paper shows that heart poisons, which are present in some species of the milkweed plant family, are ingested and stored by the monarch butterfly species that feeds on milkweeds. These butterflies, having developed an immunity to the heart poisons, use them for defense. The poisons make the insect indigestible (or at least distasteful) to many predators such as birds and spiders. The presence of these poisons in milkweeds also reduces competition for this food plant from species without immunity.

Rothschild and associates have discovered toxic or distasteful secondary substances in many insects. For example, they have found cardiac glycosides in aphids,[33] aristolochic acids in swallowtail butterflies,[34] and pyrrolizidine alkaloids in tiger moths.[35] In addition, Rothschild has shown that many butterflies secrete toxic substances themselves. One example is the burnet moth, which secretes the potent toxin hydrocyanic acid in all stages of its life cycle.[36]

Rothschild's most-cited paper is a review of secondary plant substances and warning coloration in insects.[37] This *Citation Classic*™ [38] has been cited by at least 80 researchers in the past decade. Insects with warning coloration are known as *aposematic* insects. Their bright colors alert predators to their toxicity, so predators will avoid ingesting them. Rothschild discusses the information available on those aposematic insects that take up and store toxins from food plants.

A related area of research is mimicry among insects.[39] Certain species evolve the same warning coloration, and even store the same toxins, as a successful insect "model" species. Warning coloration is directed against birds and other predators that hunt by sight. Rothschild observed that insects also produce defensive *odors* directed against predators that hunt by smell.[40] Since a number of these odors resemble each other, she concluded that mimicry of scent can occur as well as mimicry of warning coloration.

Rothschild's work in warning coloration and mimicry has vindicated the evolutionary insights of such nineteenth-century naturalists as Alfred Wallace, Henry Bates, and Fritz Müller, whose work had been wrongly discredited.[37] These scientists had intuited the presence of toxic substances in insects, but the methods of chemical analysis available at the time were too primitive to provide proof.

Through her research on butterflies, Rothschild has investigated the role of carotenoid pigments in warning or attracting other species or for camouflage. She showed that the pupae of the large white butterfly failed to match their background when their diet lacked carotenoids.[41] Normally this species is highly responsive to the color of background foliage. Also, when monarch pupae were deprived of carotenoids, they developed silver- rather than gold-flecked pupal cases.[42] In her review of carotenoids in the evolution of signaling,[43] Rothschild points out that since carotenoids are involved in both photoreception and vision throughout the animal kingdom, they must be an important factor in signal reception. She also reviews cases of both plants and animals using carotenoids in body parts displayed to warn or attract other species.

Behavior is another aspect of Rothschild's butterfly studies. She has demonstrated the large white butterfly's ability to assess the egg load on a plant or leaf.[44] The butterfly responds to visual cues, such as damaged foliage or the presence of feeding larvae. It also responds to such olfactory cues as an airborne emanation from eggs already laid on a leaf. When the butterfly detects these cues, it switches to another leaf, plant, or species. In this way, it avoids overloading the host plant and ensures an adequate food supply for the new generation.

Rothschild's fresh and startling observations put her at the forefront of a new wave of ecological research in the 1970s. Jeffrey Harborne, University of Reading, England, identified ecological biochemistry as a new interdisciplinary field that has grown up since the late 1960s. He credits Rothschild with playing a seminal role in developing this field: "By her own pioneering experiments with aposematic insects and equally her encouragement of other scientists, Dr. Rothschild has contributed more than anyone else to this new subject...."[45] (p. vi) Similarly, E.B. Ford, University of Oxford, in describing another relatively new field, ecological genetics, also cites Rothschild's contributions.[46] Ecological genetics is the experimental study of evolution and adaptation conducted in both the field and the laboratory. Ford notes, "It is to Rothschild and Clay (1952) that we owe the general analysis of brood parasitism in birds; one which has demonstrated the principles of its evolution."[46] (p. 259) He also cites her work in mimicry, plant toxins, maturation of fleas on hosts, poisons in aposematic insects, and toxic butterflies.

Rothschild has received many honors for her scientific contributions. These include the H.H. Bloomer Medal from the Linnean Society of London, which she received in 1968. She has also been made an honorary fellow of the Royal Entomological Society of London and an honorary fellow of the American Society of Parasitology. In recognition of her scientific merit, she was made a Commander of the British Empire in 1983.

Rothschild has recently been invited to deliver the Romanes Lecture for 1984-1985 at the University of Oxford. This lecture was first given in 1892 by William Gladstone. Since then, the long list of illustrious Romanes lecturers has included John Masefield, Winston Churchill, and Peter Medawar, among others.

Rothschild's memberships in professional associations include the American Academy of Arts and Sciences, the Royal Entomological Society of London, the Zoological Society of London, the Marine Biological Association of the United Kingdom, and the Linnean Society of London. She has also been a trustee of the British Museum of Natural History.

Rothschild edited *Novitates Zoologicae*, the official publication of Tring Museum, from 1938 to 1941. She has also been a member of the publications committees of the Zoological Society of London and the Marine Biological Association of the United Kingdom. She has generously edited the work of many individual scientists as well.

Rothschild's diverse scientific interests would be enough to occupy several lifetimes. But, in addition, she has supported herself, her family, and her scientific researches through farming. She considers herself a farmer as well as an experimental biologist. Her farm is situated at Ashton Wold, Peterborough, Northamptonshire, England, on an estate established by her father. Over the years, she has received a number of gold medals from the Royal Horticultural Society for fruit and vegetable cultivation. Also, the walls of one of her rooms at Ashton Wold are papered with ribbons and awards for raising prizewinning domestic animals. Her farming success has enabled her to finance all her scientific activities. In the past 60 years, she has accepted only one grant of any kind, a travel grant to a conference.

Rothschild has also been active in a broad range of civic and social causes. During World War II she joined with a group of distinguished scientists working in cryptography to crack the German secret code. She received a Defence Medal from the British Government for her work. She also aided refugee Jewish scientists during and after the war, often housing them in her own home.

Her humanitarian activities include founding the Schizophrenia Research Fund, based in London. This fund is dedicated to promoting the understanding, treatment, and cure of schizophrenia and other mental illnesses. She also helped marshal scientific evidence on homosexuality for the Wolfenden committee. This government committee produced a report[47] in 1957 that helped decriminalize homosexuality in England.

Rothschild is a strong proponent of natural resource conservation. Her latest conservation effort is to cultivate the native flora of the British Isles. To counteract the increasing encroachment of monoculture grain crops on native meadowland, she has been experimenting with growing wildflowers from seed.

Wildflowers are difficult to cultivate on a large scale, but Rothschild has developed special techniques that permit seeds to be harvested and sown elsewhere. She has recreated a Northamptonshire primitive flowering meadow containing 100 species. The Royal Horticultural Society has awarded her a gold medal for wildflower cultivation. Her efforts have generated tremendous public interest, and she is supplying seeds to other farmers and gardeners. She hopes that public bodies will adopt the practice of sowing wildflower seeds in parks and along roadsides. She recently published a book on growing wildflowers in small gardens.[48]

For some time now, it's been fashionable to deplore the specialization of scientists and other professionals in narrow subfields. Yet, as with the weather, everybody talks about overspecialization, but nobody does anything about it. Most people simply conform. Rothschild, in contrast, has dedicated her life to the untrammeled pursuit of a wide front of intellectual interests. By following her own path, she found herself at the forefront of some of the most interesting ecological researches of the 1970s. Her entire career is testimony to that most essential ingredient of original scientific research—imagination. It is a great pleasure for me to pay her a small measure of the tribute that is her due.

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