MOSQUITOES, MEDICINE AND MEMORIES[1, 2]

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Mosquitoes, medicine and memories are important factors in the lives of AMCA members: *Mosquitoes* because they form the tie that binds the society together and *medicine* for much the same reason. Their tremendous impact on human and animal health is what makes mosquitoes important. Resultantly, many of us work in medical or paramedical areas. We hold appointments as epidemiologists, medical and veterinary entomologists, arbovirologists, and parasitologists and are employed by boards of health, national and international health agencies and schools of medicine and public health. And *memories*, the third part of the title, is the storage bin of our personal and professional experiences.

In this lecture I want to share with you some of my memories, both of personal history and personal research. I will recount how I became an entomologist and involved in my particular line of research. This is not done to hold myself up as an example of how careers should be planned and developed but rather as how they really happen for many of us. I trust this will give younger people who feel confused, the hope that some semblance of order can come out of personal chaos. In all fairness though, I must add that any *order becomes apparent only in retrospect.*

I did my undergraduate work, majoring in zoology, at the University of California, Riverside. The summer after my junior year I was fortunate to obtain a job washing and waxing oranges in the laboratory of Paul DeBach, the giant in biological control. At that time all zoology majors at UCR had to do a senior thesis, so I decided to do a project related to the research in the vibrant laboratory in which I was working.

The focus of Dr. DeBach's work was the use of parasitic wasps in the genus *Aphytis* to control various scale pests of citrus fruit. The question I found absolutely fascinating was how those tiny, tiny wasps found the scales? I proceeded to do my thesis research on that question. *How do parasites find their hosts?* The results of my work didn't change the course of biological control, but being involved in original research did change the course of my life. I simply fell in love with the mental thrill, the high, of creative work. I can remember not being able to sleep because I had just devised an apparatus for testing the response of wasps to host odor—a Y-shaped glass tube. I was somewhat set back when I found that *olfactometers* had been around for a long time and I just reinvented the entomological equivalent of the wheel. The excitement remained though and I figured given time and experience, I could come up with truly original ideas.

In the fall of 1962 I started a master's program at Washington State University. I had applied to WSU because I had been told in a Denny's Coffee shop in Riverside that the school had a good zoology department. Once on campus I realized that indeed the zoology faculty was good, but not one person among them was doing the type of research of interest to me. Based on my entomological experience in DeBach's laboratory, I visited the dipteran taxonomist, Maurice James, in the Department of Entomology. I am convinced that my entomological career rests on the hearing impairment he had at the time. I asked Dr. James what the requirements would be to do a master's degree in entomology. His subsequent actions indicated that he must have thought I was completely committed to entomology at that point. Within the next few minutes he not only explained all requirements to me, but had introduced me to the department chair, Horace Telford, and had assigned me lovely office space. That treatment sure beat what I had received in zoology, so I decided to stay and see what life would be like amongst entomologists. My decision to remain was confirmed when Bob Harwood, whose research was of considerable interest to me, agreed to take me as a graduate student.

The question of how parasites find their hosts was the theme of not only the thesis work I did with Bob, but also has continued to be central to my subsequent research. The parasites have changed from chalcid wasps to mosquitoes and the hosts from scale insects to vertebrates, but the question was the same. How do parasites find their hosts?

Any behavioral pattern including host finding in mosquitoes consists of external stimuli being

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[1] Tenth Annual AMCA Memorial Lecture delivered at the 54th annual meeting of the American Mosquito Control Association, Denver, Colorado, February 22, 1988.

[2] Acknowledgments are made to the Lowndes Engineering Company and the Professional Pest Management Division of the Zoecon Corporation for their participation in sponsoring the 1988 Memorial Lecture.

received by the sense organs of the peripheral nervous system. The resulting neural information is coded and sent to the central nervous system where integration occurs, a process affected by the mosquitoes physiological state and experience. In turn a motor response is elicited that causes the observed behavior. In the rest of this lecture I will give a synopsis of what was known about each of these steps in host finding by mosquitoes before 1970 and then the major advances made in the last 20 years, essentially the time since 1970.

The observed behavior, namely, that mosquitoes blood-feed on human beings and other animals, has been known for thousands of years. Not until the early part of this century, however, did we begin to know the types of external stimuli used by mosquitoes to find their hosts. Milestones include W. Marchand's report in 1918 that female *Anopheles punctipennis* (Say) is attracted to heat, Crumb's work in 1922 that human breath as well as heat elicits a positive response from female *Culex pipiens* Linn. and R. Ko's publication in 1925 on the color preferences of Asian mosquitoes. A steady increase in the attention paid to mosquito attractants, especially as demonstrated in field studies, occurred in the 1930s and 1940s. The work of P. H. van Thiel (e.g., 1937, 1947) in The Netherlands on air-borne stimuli is prominent during this time as well as J. S. Kennedy's 1939 classic on the visual responses of flying mosquitoes.

The heyday for studies, both in the field and the laboratory, on factors involved in host attraction and discrimination were the 20 years from 1950 to 1969. Paramount among workers during this time were A. W. A. Brown and his many colleagues in Canada, P. N. Daykin, F. E. Kellogg and R. H. Wright also in Canada; A. A. Khan, H. I. Maibach, W. G. Strauss, and W. A. Skinner in the USA; J. J. Laarman in The Netherlands, U. Rahm in Germany, and Bill Reeves and E. R. Willis in the U.S. During the 1960s the first light microscopic studies on the sense organs that perceive the various air-borne external stimuli were conducted by I. A. H. Ismail (1962, 1964), E. H. Slifer (1962) and C. C. Steward and C. E. Atwood (1963). Knowledge about the central nervous system was limited to a few drawings in Christophers' 1960 classic book on *Aedes aegypti* (L.).

The next major step after identifying the types of external stimuli used by mosquitoes to locate hosts was to determine the distances over which they are operative. Mick Gillies and Tony Wilkes did the pioneer studies in this area. Mick once told me that a person is lucky to have one original idea in his or her life and his idea was the ramp trap (Gillies 1969). In the Gambia, West Africa, Mick and Tony used a number of ramp traps placed in concentric circles, each circle at a different distance from a central bait, to determine the range of attractiveness of various animals and their carbon dioxide equivalents (Gillies and Wilkes 1970, 1972, 1974). Subsequently, John Edman (1979) did a similar study in Florida.

Most of my own work since 1970 has been a systematic fine structure study of the sense organs of both sexes of *Aedes aegypti* (review by McIver 1982). Through these endeavors more is known about the structure, location and number of peripheral sense organs in *Ae. aegypti* than in any other insect. Concomitant with my structural work was the elegant neurophysiological studies of Ed Davis (review by McIver 1982). During the 1970s we determined the structure and function of most of the sense organs of adult *Ae. aegypti.*

The most significant advance in the 1980s concerned with sense organs was the demonstration of the relationship between hormones, peripheral nervous system and behavior of *Ae. aegypti.* In 1984 (a,b) Davis reported that a haemolymph-borne factor inhibited the antennal neurons sensitive to lactic acid, a well known mosquito attractant (Acree et al. 1968). In turn this decrease in sensitivity of antennal neurons inhibited host seeking behavior. The importance of this finding reaches far beyond insect neurophysiology and behavior, because it is the first demonstration in any animal of a hormone modulating behavior via a peripheral receptor system. In 1987 Marc Klowden, Ed Davis and Mary Bowen demonstrated the fat body to be the source of this hormone.

In depth structural analyses of the mosquito brain was started in the 1980s. For *Ae. aegypti* the deutocerebrum of the female was studied by Childress and McIver (1984) and the brain and suboesophageal ganglion of the male by J. M. Nyhof and myself (unpublished data). This type of work is necessary for understanding the integration of sensory information.

Mosquitoes, medicine and memories—among my most pleasant personal memories will be the honor of being the 1988 AMCA Memorial Lecturer.

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