ARTICLES

ARE MOSQUITOES GOURMET OR GOURMAND?[1,2]

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ABSTRACT. The scientific contributions of Professor Brian Hocking are summarized, especially his writings on the specificity of blood feeding. Mosquito host-seeking behavior and feeding success are discussed within the context of human pest and vector species and in light of anticipated social and environmental changes.

THE MAN WE HONOR

Last year an adopted Canadian, Dr. Susan McIver, presented the memorial lecture so it seems rather fitting that this year AMCA has extended its recognition of the contributions of its membership from the North Country one step further as we memorialize a distinguished Canadian scientist, Professor Brian Hocking. This is the first time that the Committee has chosen to honor a deceased culicidologist from Canada, and I personally can think of no one who is more deserving than this quick-witted, sometimes scruffy-looking pioneer whose untimely death from cancer robbed the entomological community and literature of one of its most insightful contributors. A few months before his death, Dr. Hocking received the Gold Medal Award—the highest honor given by the Canadian Entomological Society.

The forests and tundras of the far north are where Dr. Hocking's interests in biting flies were generated and molded. Those unbridled summer experiences early in his career (Fig. 1) and his subsequent writings exploiting and expanding on those experiences are what I wish to focus or today. I am pleased to have been asked to give this lecture for several reasons, but particularly on two accounts. First, my own thinking about mosquito blood-feeding behavior has been profoundly influenced over the past 24 years by the work of Professor Hocking. In a few moments I will share some of those thoughts with you. Secondly, I feel fortunate to have had the opportunity to briefly know Brian and his wife Jocelyn and to share my laboratory in Vero Beach (and my in-law's mobile home) with them for several weeks near the end of Brian's career.

My personal view of dedication and determination had to be revised after watching this frail, terminally ill man sitting at the microscope for hours identifying the previous night's collection of insects with beads of perspiration on his forehead. He was struggling to finish the field evaluations of his latest invention—a wind-controlled directional insect trap. Periodically he would bolt for the men's room when he could no longer contain nor ignore the constant nausea. In the end, he was forced into the local hospital and the Royal Canadian Air force sent a hospital plane to Florida to retrieve their gallant friend. Once in the familiar air of Edmonton he found new strength and, I am told, was soon driving himself to work with an intravenous apparatus suspended from the passenger seat and attached to his arm. How many of us would have the physical and mental fortitude to stay focused on our work under such circumstances? I would venture to guess, very few.

To be sure, Dr. Hocking had been taught the lesson of discomfort by the hordes of northern *Aedes* and *Simulium* during his many summers of research in the subarctic. From the late 1940s through the early 1950s he was actively involved in the testing of candidate repellents since he thought this to be the most realistic strategy for dealing with the hordes of biting flies in the vast, isolated North Country (Fig. 2). In one such evaluation, his untreated control forearm' reportedly attracted 289 biting *Aedes* in a one-minute test (Fig. 3). This is *real* discomfort!

Over several summers early in his career, Professor Hocking conducted research on the biology and control of northern *Aedes* and black flies, mainly at the Churchill Field Station near the Hudson Bay, under the sponsorship of the

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[2] Acknowledgments are made to The Lowndes Engineering Company and the Professional Pest Management Division of Zoecon Corporation for their participation in sponsoring The 1989 Memorial Lecture.

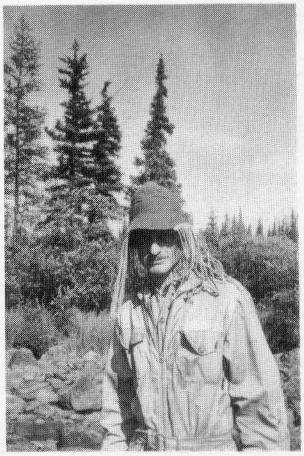

Fig. 1. Dr. Hocking dressed for field work in northern Canada.

Fig. 2. Dr. Hocking and crew preparing for a field test of mosquito repellents.

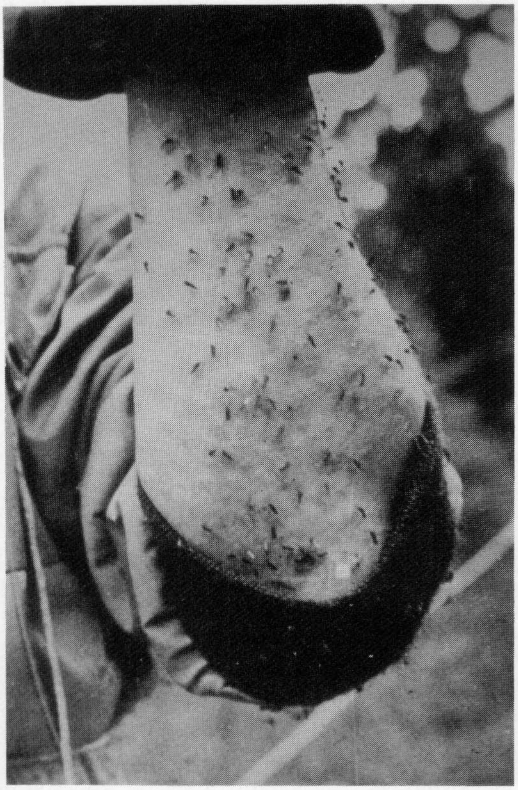

Fig. 3. Hocking's untreated forearm after a repellent test.

Canadian Department of Defense (Fig. 4). These years, more than any others during his distinguished career, seem to have influenced Brian's thinking about the behavior of biting flies and particularly about their dispersal and the way in which they locate their hosts.

Professor Hocking was an imposing man of high scientific principles and with high expectations of those around him. His intimidating aura caused many a novice student to live in near mortal fear of him until discovering that, although never to be taken lightly, his bark was considerably worse than his bite. However, Hocking was not a brash man or one to reach conclusions without considerable thought; therefore, he was not easily persuaded to abandon his position. A story related to me by one of his former students gives some insight into this side of Brian's character. A corduroy road of spruce logs was being built across a bog near the

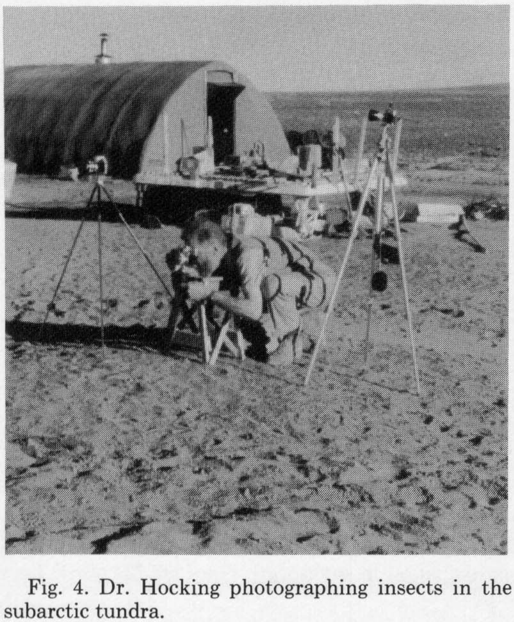

Fig. 4. Dr. Hocking photographing insects in the subarctic tundra.

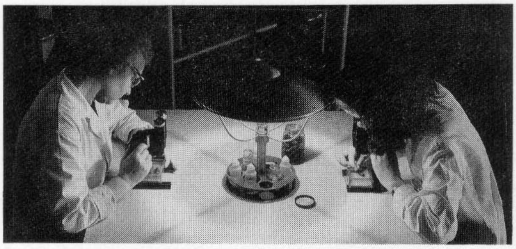

Fig. 11. Hocking's four-station student microscope table.

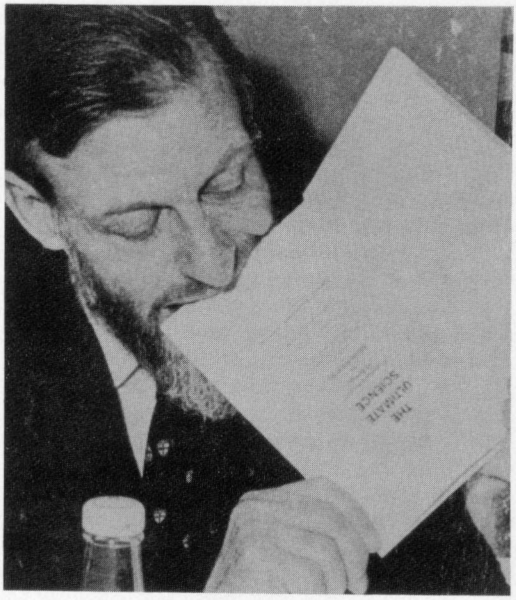

Fig. 12. Professor Hocking "eating his own words."

observe, list on paper, and turn in at the end of his nose-picking, body-scratching, beard-pulling performance. The student who spotted the most errors was to receive a book prize. But when the prize was being awarded to the eager winner, who had observed over 40 faux pas, the professor seemed a bit miffed. Apparently, the over zealous student had included on his list several minor sins that Professor Hocking regularly committed during normal lecturing.

HIS CONTRIBUTIONS

The list of Dr. Hocking's publications is long and varied. Time does not permit even a brief summary of his many contributions to the scientific literature. Instead I would like to focus for a moment on just one of his publications, the one which is most relevant to the topic I have chosen to speak on today: the feeding specificity of mosquitoes. This article, "Blood-Sucking Behavior of Terrestrial Arthropods" (1971), was his second *Annual Review of Entomology* article and was more introspective than his first on 'Northern Biting Flies," written 11 years earlier. He did not simply review the literature but tempered it with his own experiences and drew insightful inferences from it. For example:

"More than half the literature on blood-sucking arthropods relates to mosquitoes and nearly half of this relates to *Aedes aegypti* or the *Culex pipiens* complex . . . these two species are far from representative of mosquitoes."

In terms of mosquito feeding behavior, this statement is probably still true today, and it is a fact that we need to constantly keep in mind as we read the literature.

Another of Hocking's blunt observations in this review paper that needs reiteration is the following:

"There are many hundreds of papers on the physiological responses of blood-sucking arthropods, especially mosquitoes, in the laboratory to the various stimuli supposedly provided by their hosts, and hundreds more ecological studies on the mechanisms of host finding and selection in the field. Rarely has so much work yielded so little consensus of opinion; results which are apparently contradictory abound, even in the same paper. . . .

From this Hocking concluded (and I have added parenthetically) the following:

"Rudolfs' 1922 assessment of the host-finding procedure in mosquitoes is remarkably similar to that of Clements' in 1963" (and those still being written in 1989).

In his 1971 review article, Hocking attempted to summarize in a very general way the principal stages in securing a blood-meal and the stimuli controlling each stage. I will reexamine this process in some detail in a moment, but for now the important thing is that this mental exercise apparently led Hocking to conclude the following (parenthetical note added by author):

"It is clear that at least some of the steps in the host-finding process are links in a chain reflex. An experimental study which starts in the middle of a chain (or near the end as with most olfactometers) will yield very different results from one which starts at the beginning."

THE HOST-SEEKING PROCESS

A sustained response to a continuum of reinforcing stimuli is still the most useful framework in which to view host-seeking behavior.

Figure 13 is yet another attempt to illustrate this process. Two different strategies are indicated.[3] Most mosquitoes actively search for hosts a-washbowl black fly rearing apparatus (Figs. 9 and 10), early wind tunnels for studying insect flight and a glass-top, lab-table which accommodated 4 microscopes yet required only a single upper and lower light source (Fig. 11), all wonderfully clever inventions motivated by a creative but thrifty man forced to operate under tight budgets.

Dr. Hocking was a vigorous advocate of biological literacy for the entire citizenry and took particular interest in secondary school education. He taped nearly 70 radio and TV programs on scientific topics, wrote several laboratory manuals and helped develop a rigorous science curriculum for the Edmonton public schools. All three books that Professor Hocking wrote were aimed toward developing biological awareness among the lay readership to which they were targeted.

But Dr. Hocking was not a man without a sense of humor. To realize this fact, one need only read his many editorials in *Quaestiones Entomologicae* (the scientific journal he initiated) or look at the picture on the back cover of his second book *(Science or Oblivion)* showing him "eating his own words" (Fig. 12). He was the frequent butt of jokes and gag gifts around the department, especially at the annual Christmas party. Professor Hocking once presented a seminar on public speaking to graduate students in which he deliberately committed many errors of style and etiquette which students were to

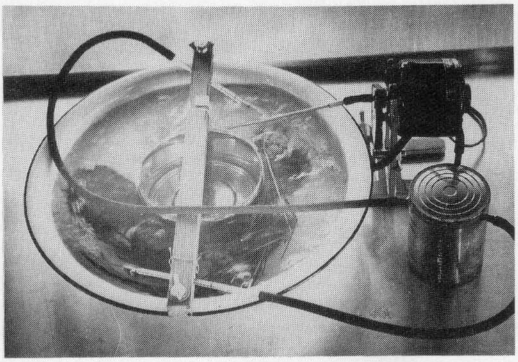

Fig. 9. Black fly rearing apparatus.

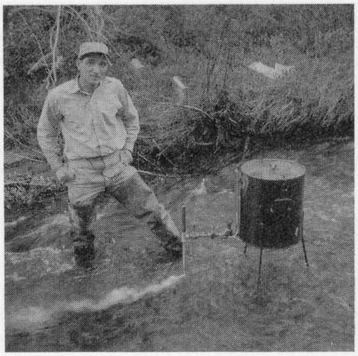

Fig. 7. Hocking's drip can for dispensing DDT in streams to control black flies.

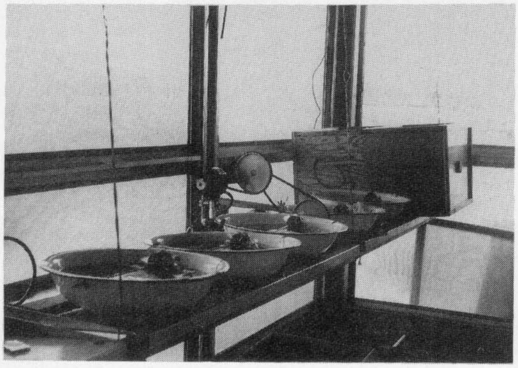

Fig. 10. Series of "stream-in-bowl" for evaluating DDT against black fly larvae.

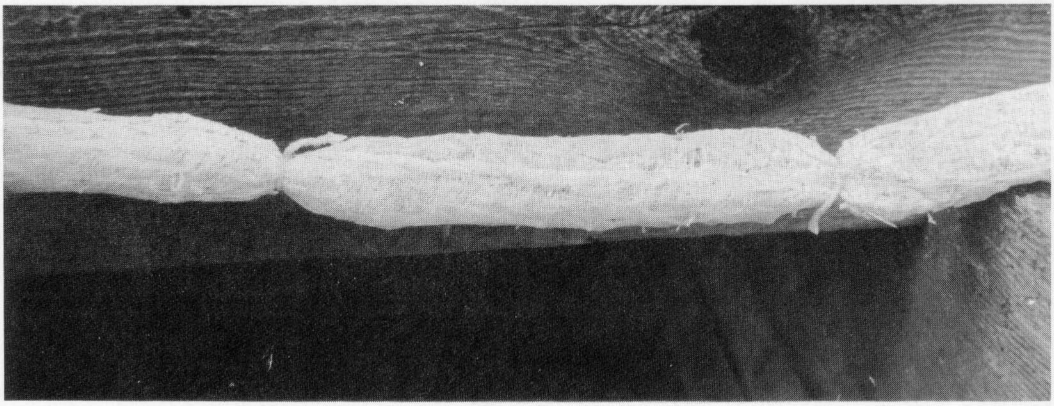

Fig. 8. Hocking's DDT sausage consisting of DDT and plaster of Paris.

George Lake Field Station late in the summer. The grousing of the student slave labor was getting intense. To them, the task seemed futile since the provincial Department of Transportation was planning a new road in the spring. The student assigned the job of digging a drainage ditch leading away from the new log roadway through the bog had surprisingly encountered permafrost only 3 feet beneath the surface. Unable to dig any deeper, he abandoned his shallow trench and assumed the familiar "lean on shovel" stance. When Professor Hocking returned to the work site he immediately spotted the idle student and began grilling him about the unfinished ditch. The student's permafrost excuse brought a disbelieving look of disgust to Hocking's face as he grabbed the shovel and swung it vigorously into the trench bottom. His expression quickly turned to one of surprise and confusion as the spade reverberated from the impact of hitting frozen muck. (permafrost should not have been that shallow this far south.) "Huh!!?? I suspect you may be right," Hocking retorted still leaving the door open to the faint possibility that the student had buried a chunk of ice in the bottom of his trench just to get out of work.

Fig. 5. DDT trials with a flit gun.

Professor Hocking was not one to only concern himself with the puritan side of science. He was not above mucking about in the field and applying some of his science in trying to control biting flies. Besides the keen interest in repellents already mentioned, he was involved in the post-war testing of DDT to control mosquitoes and black flies around military installations in the far north. This was something that Brian, an ardent lover of nature, probably looked back on with some trepidation in later years. Starting with a flit gun (Fig. 5), he eventually tested both ground and aerial adulticide applications (Fig. 6) and designed one of the earliest drip cans for dispensing larvicide into streams to kill black flies (Fig. 7).

Professor Hocking was an inveterate inventor and master gadgeteer. He developed, among other things, "the DDT sausage" for slow insecticide release into streams (Fig. 8), a stream-in-

Fig. 6. Aerial DDT trials.

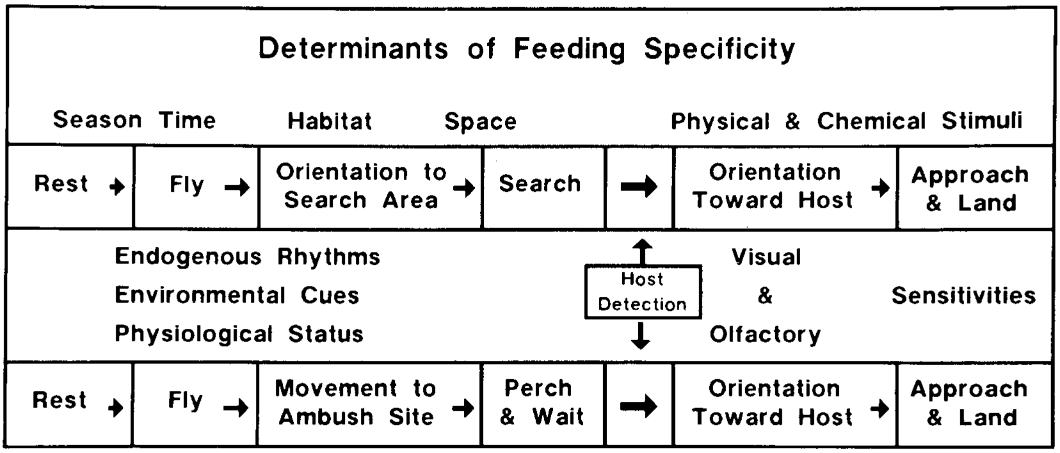

Fig. 13. Illustration of the mosquito host-seeking process from initial flight to arrival near the host. Both searching and wait-in-ambush strategies are indicated.

during prescribed periods in the field. However, diurnal species appear instead to wait until some visual or olfactory host-related information is received and then embark on orientation flights directed toward the host as shown in the bottom line of this illustration (Fig. 13).

Nature is unlikely to sustain very many false starts. Therefore, the notion that host stimuli become increasingly more meaningful and that the mosquito's responses to those stimuli intensifies if the approaching host is a suitable one but declines if it is not, must certainly be false. If this were not so, mosquitoes would continuously be wasting their limited time and energy flying down blind alleys seeking out unacceptable hosts. Nature is seldom so inefficient. It would be akin to our walking a mile to a pizza parlor and then deciding we prefer to eat Chinese food. We may do this occasionally, especially if the parlor is closed or the restaurants are next to each other, but certainly not regularly.

Even if we can accept the functional concept that host discrimination normally occurs before orientation takes place, the question remains: how much innate discrimination actually takes place and how is it accomplished? Are unacceptable hosts simply not detected?... or are they detected but then behaviorally rejected because they lack critical stimuli or sensory inputs needed for anemotaxis to occur? Unacceptable hosts may even be repellent, but there is little supporting evidence for this idea. And what about the seemingly more preferred hosts within the broad range of hosts that are acceptable to a mosquito? Do they somehow illicit a stronger response than do less preferred hosts when they are first detected by the mosquito?... or are mosquitoes simply able to detect them from a greater range or follow their odor plumes more efficiently?

In the laboratory, the capacity to discriminate can be tested by simultaneously exposing mosquitoes to two different plumes of airborne stimuli and then observing the behavioral choices that are made. But few species are willing to submit to these "taste tests," and one can not help but question whether this format is at all comparable to what host-seeking mosquitoes encounter in nature. *Aedes aegypti* may prefer hot Ping-Pong balls to cold ones or fingered marbles to clean ones in a lab-box, but they probably pay little attention to either item in the real world regardless of how hot or smelly.

We are all aware of a few well documented cases of gourmet feeding by mosquitoes. Examples such as the frog-feeding *Culex territanz*, fish-feeding *Uranotaenia lateralis* and bird-feeding *Cx. restuans* and *Culiseta melanura* immediately come to mind (Tempelis 1975). But these are insects that generally have become structurally and functionally specialized (McIver 1982) and ignore other kinds of hosts even when caged together for days. The literature can be rather misleading on this point. Papers are published highlighting the one or two misguided *Cs. melanura* that are taken in many hours of human biting collections, when the real epidemiological significance lies in the hundreds of human bait collections which failed to turn up a single spec-

[3] Species that normally search for hosts also may feed opportunistically when hosts happen to enter their resting habitat. This sort of 'baited' feeding may account for the unusual blood meals that are sometimes detected in otherwise quite monophagous feeding patterns.

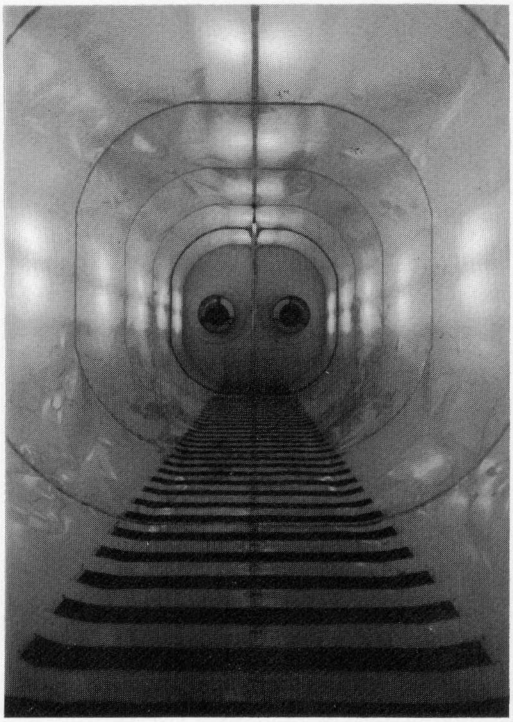

Fig. 14. Ten-meter long by 2 meter diam experimental wind tunnel built by the author to study host-seeking behavior.

imen. In the scientific community, we have an aversion to publishing negative results while we relish reporting rare events and trying to convince ourselves and others that they represent something highly significant. A good case in point is the cancer risk to children that has been fantasized and publicized recently because of Alar® (daminozide) traces occasionally found on apples. While government officials consider a total ban on Alar, hundreds of thousands of people are dying annually from government subsidized cancer. The fact that L-lactic acid has attractant properties for *Ae. aegypti* in the laboratory is published in *Science* and cited often, while data on its subsequent failure to enhance attractancy under field conditions collects dust in our files and receives little attention. I think the time is overdue to start a new journal exclusively devoted to publishing experiments and techniques that did not work. Think of all the time and money that could be saved if we knew about each others failed experiments as well as our exaggerated discoveries. I will attempt to set the stage for this by sharing with you one of my own failures.

I was once convinced that the solution to understanding the host selection process in mosquitoes was to build an automated, environmentally controlled wind tunnel of sufficient size and character to allow observation of the entire host-seeking process in diurnal, crepuscular and nocturnal mosquito species. I backed up this conviction with months of construction and about 4 years worth of preliminary experiments (Fig. 14). The basic plan was to simultaneously compare the flight responses of so-called specialists and generalist feeders to the wind-borne emanations and visual cues (or both) from a wide variety of intact animals. Tantalizing but too often unreproducible or unexplainable results eventually caused me to cast my net in a different direction.

GOURMET OR GOURMAND?

Although we can conclude that there are a few highly specialized species that have become highly adapted for feeding selectively on a very narrow range of hosts, we must still admit to ignorance concerning the mechanisms employed by these species in seeking out their unique hosts. Since these species are generally of little economic or medical importance and are often difficult to work with in the laboratory, it may be years before we understand the physiological and behavioral mechanisms which underlie and maintain this feeding specificity.

But what about the great majority of mosquitoes, including those human pest and vector species which so concern mosquito control and health agencies? How discriminating are these species? Do they tend to be gourmet or gourmand? Our honoree, Professor Hocking, had something to say about this question that merits repeating here:

"The phenomenon of blood-sucking is not in general a specific one. A single species may feed on several species of reptiles, birds, mammals and amphibia . . . but at a given time in a given habitat there is commonly a single obvious host. Through techniques such as the precipitin test, this gives an illusion of specificity, and since only the olfactory sense has the versatility to account for specificity, much effort has been devoted to finding a specific attractant emitted by the animal we are most interested in—MAN.

"Every imaginable part of the human body and its products must by now have been fractionated in every possible way in the search for a specific chemical attractant. While certain attractive materials have been found . . . nothing proves to be as attractant as the intact man."

"This seems to suggest that blood-sucking arthropods recognize man for what he is, by his complex of effluvia and not by any specific indicator. Only this can explain the evident discrimination by mosquitoes between men, women and children, between one race and another, and even between one individual and another. This simply means that the kairomone is a complex mixture. . . ."

Most of us probably agree with Hocking's basic conclusion that a mosquito must detect and find its host through a sensory network that is capable of receiving and processing a complex mixture of stimuli. Unfortunately, the task of experimentally dissecting away and understanding this neuro-behavioral system has been painfully slow with little substantial progress in the nearly 20 years since Hocking wrote his review. However, the evidence that he alluded to concerning certain individuals being more attractive than others has served to focus our attention where it belongs when it comes to disease transmission. As with the AIDS virus, where one highly infectious and promiscuous individual can spawn a mini-epidemic, so might it be with certain mosquito-borne diseases where infectious hosts may attract (perhaps because of elevated body temperature) and provide bloodmeals for unpredictably large numbers of mosquitoes. Preliminary field data from Australia (Mahon and Gibbs 1982) suggested that hens infected with Sinbus virus attracted more mosquitoes than uninfected ones. In recent studies in Thomas Scott's laboratory at the University of Maryland, we have examined this issue further with house sparrows infected with Eastern, Western or St. Louis encephalitis virus. At least within the confines of the laboratory, no enhanced attraction could be credited to viral infection (Scott et al., in press).

A related question concerning age differences in attractancy has long been debated, especially in terms of malaria transmission. Although young animals may be smaller targets for mosquitoes, they represent the major portion of the susceptible pool of non-immunes in the host population (Edman and Scott 1987). Again in Tom Scott's laboratory, we examined this question with adult and nestling house sparrows. As with human infants in malaria studies, nestling sparrows proved to be olfactorally less attractive under these short-range test conditions (Scott et al., in press).

FEEDING SUCCESS

One thing we have come to better appreciate since Hocking wrote his review on blood-feeding behavior is that the feeding process does not terminate with the location of a suitable host. Since it is reproductive success that drives evolutionary change, what happens after hosts are located really directs the biological events which lead the mosquito to the host in the first place. For example, mechanisms for selective feeding on humans would never evolve unless females that opportunistically feed on humans are more successful reproductively than their sisters attempting to feed elsewhere.

The fact that there are so few examples of gourmet feeding among the some 3,000+ known species of mosquitoes (and that autogeny persists in so many) suggests that successful bloodfeeding is no routine matter. Finding hosts, especially when they are small or scarce, clearly represents an obstacle that many females fail to overcome.

Obtaining a blood-meal from an active, sensitive vertebrate once it has been detected and approached, has its own hazards. There are probably no completely safe hosts. Hosts such as cattle and night herons may be more receptive targets than most (Edman and Scott 1987, Edman and Spielman 1988), but even they have limits to their tolerances. Crowding behavior in cattle is a common expression of these limits.

The second half of the feeding process, the half which is highly regulated by the host, is depicted in Fig. 15. Defensive behavior, which varies with mosquito density and with host age, species, health, etc., can abort the feeding process anywhere along the sequence. However, interruption appears more likely to occur at certain points. The host may interfere with landing if an approaching mosquito is seen or heard. Landing and foraging for a feeding site are frequently detected tactually and cause defensive movements by the host. Painful contact with subdermal nerve endings during probing with the fascicles often elicits the most vigorous defensive reactions from hosts. Pause is a behavior which appears to have evolved in some mosquitoes as an escape valve due to the probability of detection associated with landing on their highly defensive hosts (Walker and Edman 1985a). Thus, some species normally freeze momentarily after landing to assure they have not been detected by the host before commencing to forage and probe. Mosquitoes are least likely to be disturbed during actual blood uptake were it not for other individuals landing and probing nearby eliciting movements from the host which coincidentally disturb gorging females as well. Evidence for this can be seen from the increasing number of partially fed mosquitoes observed as the biting density increases (Edman et al. 1972). Further evidence that this sort of feeding interruption followed by refeeding on other hosts takes place in nature has recently been obtained by a graduate student in my laboratory working with *Cs. melanura* and avian hosts marked with alkali metals (Anderson and Edman, unpublished data), and for Puerto Rican *Ae. aegypti* (Scott, personal communication) that were examined histologically (Romoser et al., in press) for signs of multiple feeding.

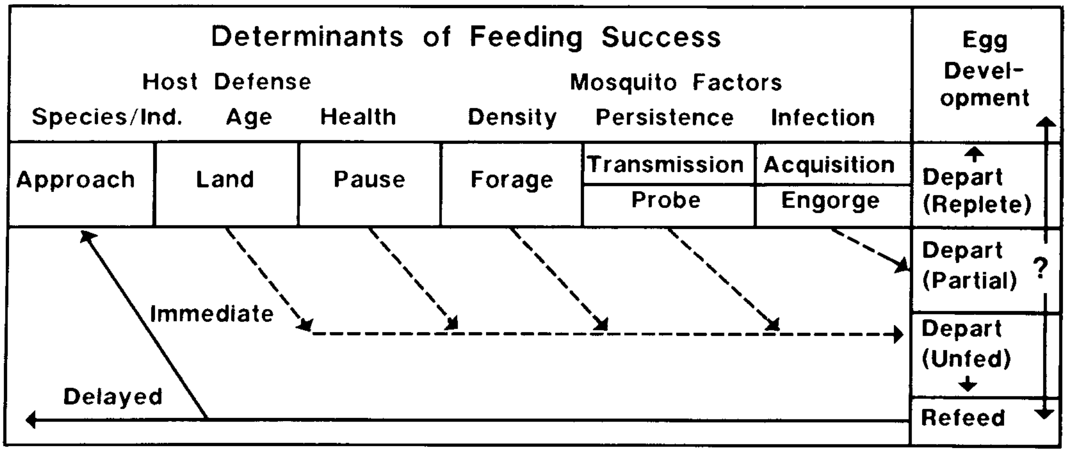

Fig. 15. Illustration of the final phase of the feeding process which is highly regulated by the host.

Persistence (Walker and Edman 1985b), as well as other features of mosquito biting behavior not listed on Fig. 15 (e.g., night feeding, ankle feeding), appear to have evolved to increase feeding success on more defensive hosts.

An aspect of host defensive behavior that has long interested me has to do with host health and whether viremic/parasitemic individuals are fed on selectively due to their reduced defensiveness. It is well known that sick animals generally have more ectoparasites due to the reduction in grooming. It is therefore logical to question why the same would not apply to antimosquito behavior. If the illness were caused by a mosquito-borne agent, the epidemiological implications are quite obvious. Jon Day first tested this idea in my laboratory with rodent malaria models, and the results were highly encouraging (Day and Edman 1983, Day et al. 1983). Turell et al. (1984) observed a similar phenomenon with Rift Valley fever virus infected lambs which was partially correlated with elevated temperature but also, in older lambs, with behavioral changes. More recent experiments with house sparrows infected with arbovirus have been less encouraging because the adult birds tested failed to show any symptoms of disease (Scott et al. 1988). Nestlings became acutely ill and died, but they were not defensive to begin with, thus feeding success could not be further enhanced through their illness. Perhaps fledgling birds are the critical part of the story since both attractiveness and defensiveness are approaching maturation around the time birds fledge (Scott and Edman, in press). The viremic response of fledgling birds needs further investigation as well as the effect of mosquito density on feeding success during this potentially dynamic period for transmission.

Parasite infection in the mosquito also can affect feeding success (Fig. 15). Although more subtle than in plague transmission by the blocked flea, salivary gland pathogens such as malaria and arboviruses can result in increased probing time and subsequently, aborted feeding and multiple host encounters (Edman and Spielman 1988). If forced off the host with little or no blood, these infected females—having already injected their infective saliva, will soon be attempting to feed again, perhaps on another susceptible host. In contrast, females that obtain replete blood-meals wait several days to develop and oviposit their eggs before reentering the pool of actively feeding vectors.

CHANGING FEEDING PATTERNS

If defensive hosts cause significant levels of unsuccessful feeding, then fewer mosquito species should be attracted to such hosts and, among those species that are attracted, special mechanisms for circumventing host defensive behavior should have evolved. In fact there is evidence to suggest that both may be true (Edman 1988). Although we naked apes may look like easy sources for mosquito blood-meals, the control equipment being displayed at this meeting indicates that we have clearly carried our defensiveness to a level of sophistication not seen in any other species. Moreover, our blood is not very nutritious, apparently due to low levels of the essential amino acid isoleucine (Woke 1937, Edman and Spielman 1988). Equivalent amounts of human blood have produced significantly fewer eggs in every species tested (Edman and Spielman 1988), and more human blood is also required to initiate egg development (Edman and Kay, unpublished

Table 1. Some general biological characteristics of the two major groupings of mosquito species that attack humans.

Biological attribute	Human pests (gourmand)	Human vectors (gourmet tendencies)
Primary hosts	Large	Small
Activity	Crepuscular	Nocturnal (or diurnal)
Flight habitats	Exposed	Protected
Dispersal	Strong	Weak
Numbers	Large	Modest
Immature habitats	Temporary water	Semipermanent water

data). Hence, compared with other hosts, small interrupted blood-meals involving humans are more likely to result in multiple feeding, vis-a-vis partial egg development.

This might lead one to wonder why mosquitoes bite humans at all and why mosquito-borne diseases such as malaria and dengue are on the rise. If we consider the species that commonly bite us, some broad generalizations can be made and species placed into two basic categories (Table 1). The first includes the gourmand pest species which normally feed on large mammals in open areas around dusk. Although their great numbers and indiscriminant attacks cause us great discomfort, they are not well adapted for feeding successfully on defensive hosts and could never sustain their high densities if they had to depend on humans for blood. They are not efficient vectors of any human pathogen but may occasionally pass on zoonotic infections. The second group has not been as successful numerically because they have mostly evolved to exploit forest habitats (usually in the tropics) and they have developed adaptations for nocturnal[4] feeding on smaller and consequently more defensive animals such as birds, rodents and primates. There is a general correlation between host size, defensiveness, and mosquito feeding success on unrestrained individuals (Edman and Scott 1987).

In the last few 100 years human populations and urbanization have increased dramatically; we are currently in our third major growth phase (Edman 1988). Due to population pressure, forests are being cleared for fuel and agriculture at an alarming rate. Wild hosts are displaced and those forest mosquitoes that are able to adapt to our environmental disruptions often find that humans and their domestic animals are just about the only "game" left in town. As long as ample livestock coexist with humans, the more gourmet mosquito species will continue to only feed nominally on people, and disease transmission should be maintained at endemic levels. However, when livestock are absent, as in much of the African tse tse belt, and when beasts of burden like the water buffalo in rice paddies are replaced by "iron buffaloes," as in parts of Asia, the choice becomes narrower; and humans become a principal target and epidemic levels of disease transmission can be expected. Since the ancestral hosts of these forest mosquitoes were small and defensive, these species often have adaptations which considerably increase their feeding success on humans as well (Edman 1988).

Late-night, indoor feeding by certain *Anopheles* and landing on ankles and elbows by day-feeding *Ae. aegypti* are prominent examples of how some of these species are continuing to adapt to the pressure of becoming increasingly dependent on human beings for their blood-meals. Mosquitoes have always had the capacity to develop into more gourmet blood-feeders, but the scarcity and/or instability of most vertebrate populations throughout history seems to have weighed against such a strategy for most species. Current trends in land use and host populations suggest that the best evolutionary strategy for mosquitoes in the past may not be the best strategy for the future.

Our ability to successfully defend ourselves against mosquito feeding can play a significant role in this ongoing evolutionary process. We need new defensive weapons, especially against the increasingly anthropophilic vector species. Professor Hocking was convinced that repellents were perhaps the ultimate solution. Highly effective repellents would serve to actively select against human feeding behavior. In cases where humans are nearly the only host available, effective repellents would either select for autogeny or lead to extinction. Emerging molecular and neurobiological technologies seem to make this an ideal time to reinvest in highly directed studies to develop a new generation of repellents based on a full understanding of how mosquitoes sense and locate their hosts and how to best short circuit critical chemical messages. Clearly, the answers will not be found by merely looking

[4] Note: a few important species such as *Aedes triseriatuz, Ae. albopictus* and *Ae. aegypti* feed diurnally.

at the peripheral receptors as we have in the past. We must get inside the central nervous system where information in processed and outputs are controlled.

ADDENDUM

Since we are meeting in Boston and I live just down the road, I can hardly close without some reference to New England. Mosquito control has always been somewhat controversial in this part of the country except perhaps near saltmarshes or during outbreaks of EEE. The following quotation from one of Massachusetts' most famous citizens seems to typify the more stoic downeast view of mosquitoes; it seems like an appropriate way to end.

"Do what we can, summer will have its flies If we walk in the wood, we must feed mosquitoes."—Ralph Waldo Emerson

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REFERENCES CITED

Day, J. F. and J. D. Edman. 1983. Malaria renders mice susceptible to mosquito feeding when gametocytes are most infective. J. Parasitol. 69:163–170.

Day, J. F., J. D. Edman and K. Ebert. 1983. Feeding patterns of mosquitoes simultaneously exposed to malarious and healthy mice, including a method for separating blood meals from conspecific hosts. J. Med. Entomol. 20:120–127.

Edman, J. D. 1988. Disease control through manipulation of vector-host interaction: some historical and evolutionary perspectives. Misc. Publ. Soc. 68:43–50.

Edman, J. D. and T. W. Scott. 1987. Host defensive behavior and the feeding success of mosquitoes. Insect Sci. Applic. 8:617–622.

Edman, J. D. and A. Spielman. 1988. Blood feeding by vectors: physiology, ecology, behavior and vertebrate defense, p. 153–189. *In*: T. Monath (ed.). Epidemiology of arthropod-borne viral diseases, Vol. 1. CRC Press, Inc., Boca Raton, FL.

Edman, J. D., L. A. Webber and H. W. Kale. 1972. Effect of mosquito density on the interrelationship of host behavior and mosquito feeding success. Am. J. Trop. Med. Hyg. 21:487–491.

Hocking, B. 1971. Blood sucking behavior of terrestrial arthropods. Annu. Rev. Entomol. 16:1–26.

Mahon, R. and A. Gibbs. 1982. Arbovirus infected hens attract more mosquitoes, p. 502–504. *In*: J. S. Mackenzie (ed.). Viral diseases in South East Asia and the eastern Pacific, Academic Press, Sydney.

McIver, S. B. 1982. Sensilla of mosquitoes (Diptera: Culicidae) J. Med. Entomol. 19:489–535.

Romoser, W. S., J. D. Edman, L. H. Lorenz and T. W. Scott. Histological parameter useful in the identification of multiple blood meals in mosquitoes. Am. Soc. Trop. Med. Hyg. (in press).

Scott, T. W., L. H. Lorenz and J. D. Edman. The effect of house sparrow age and arbovirus infection on attraction of mosquitoes. J. Med. Entomol. (in press).

Scott, T. W., J. D. Edman, L. H Lorenz and J. L. Hubbard. 1988. Effects of disease on vertebrate's ability behaviorally to repel host-seeking mosquitoes. Misc. Publ. Entomol. Soc. Am. 65:9–12.

Tempelis, C. H. 1975. Host-feeding patterns of mosquitoes with a review of advances in analysis of blood meals by serology. J. Med. Entomol. 11:635–652.

Turell, M. J., C. L Bailey and C. A Rossi. 1984. Increased mosquito feeding on Rift Valley fever virus infected lambs. Am. J. Trop. Med. Hyg. 33:1232–1238.

Walker, E. D. and J. D. Edman. 1985a. Feeding sites selection and blood feeding behavior of *Aedes triseriatus* (Diptera: Culicidae) on rodent (Sciuridae) hosts. J. Med. Entomol. 22:287–294.

Walker, E. D. and J. D. Edman. 1985b. Influence of host defensive behavior on mosquito biting persistence. J. Med. Entomol. 22:370–372.

Woke, P.A. 1937. Comparative effects of the blood of different species of vertebrates on egg production of *Aedes aegypti* Linn. Am. J. Trop. Med. 17:729–745.