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SYMPOSIUM ON
BITING FLY CONTROL AND ENVIRONMENTAL QUALITY

SYMPOSIUM SUR LA
LUTTE CONTRE LES MOUSTIQUES ET LA QUALITÉ DE L'ENVIRONNEMENT

Organized by the University of Alberta, Department of Entomology
and the Advisory Committee on Entomological Research to the
Defence Research Board

ORGANIZING COMMITTEE

Brian Hocking
Anne Hudson
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BITING FLY CONTROL AND ENVIRONMENTAL QUALITY

Proceedings of a Symposium
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Anne Hudson

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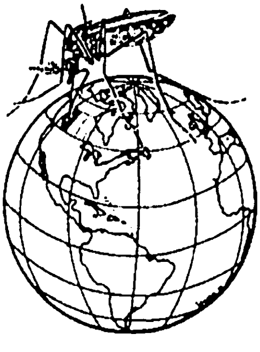


STATEMENT OF THE PROBLEM

AREA CONTROL

Conventional chemical control

Unconventional chemical control

Monitoring and assessment

Biological control

PROTECTION OF INDIVIDUALS

Personal protection

Behaviour and ecology of populations

CONTRIBUTORS

J.R. Anderson
Division of Parasitology, College of Agricultural Sciences, University of California, Berkeley, California, U.S.A.

W.F. Baldwin
Atomic Energy of Canada Limited, Chalk River, Ontario.

E.C. Bay
Department of Entomology, University of Maryland, College Park, Maryland, U.S.A.

R.E. Bellamy
Canada Department of Agriculture, Research Branch, Saskatoon, Saskatchewan.

J. Bělicěk
Department of Entomology, University of Alberta, Edmonton, Alberta.

R.A. Brust
Department of Entomology, University of Manitoba, Winnipeg, Manitoba.

H.C. Chapman
Entomology Research Division, Agricultural Research Service, U.S. Department of Agriculture, Lake Charles, Louisiana, U.S.A.

M.F. Coffey
Canadian Armed Forces Northern Command, Yellowknife, N.W.T.

G.S. Cooper
Cyanamide of Canada, 1 Cityview Drive, Rexdale, Ontario.

P.S. Corbet
Department of Biology, University of Waterloo, Waterloo, Ontario.

G.R. DeFoliart
Department of Entomology, University of Wisconsin, Madison, Wisconsin, U.S.A.

J.A. Downes
Canada Department of Agriculture, Entomology Research Institute, Carling Avenue, Ottawa, Ontario.

J.J. Fettes
Chemical Control Research Institute, Canadian Forestry Service, Department of Environment, Ottawa, Ontario.

R. Frank
Department of Agriculture and Food, University of Guelph, Guelph, Ontario.

F.J.H. Fredeen
Canada Department of Agriculture, Research Branch, Saskatoon, Saskatchewan.

C.R. Harris
Canada Department of Agriculture, Research Institute, University Sub Post Office, London, Ontario.

W.O. Haufe
Canada Department of Agriculture, Research Branch, Lethbridge, Alberta.

B. Hocking
Department of Entomology, University of Alberta, Edmonton, Alberta.

Anne Hudson
Canada Department of Agriculture, Entomology Research Institute, Carling Avenue, Ottawa, Ontario.

J.E. Hudson
Department of Entomology, University of Alberta, Edmonton, Alberta.

C.L. Judson
Department of Entomology, College of Agricultural and Environmental Sciences, University of California, Davis, California, U.S.A.

M.A. Khan
Canada Department of Agriculture, Research Branch, Lethbridge, Alberta.

M. Laird
Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland.

L.P. Lefkovitch
Canada Department of Agriculture, Statistical Research Service, Carling Avenue, Ottawa, Ontario.

I.S. Lindsay
Defence Research Board, Defence Research Establishment, Ottawa, Ontario.

G.A.H. McClelland
Department of Entomology, College of Agricultural and Environmental Sciences, University of California, Davis, California, U.S.A.

Susan McIver
Department of Parasitology, School of Hygiene, University of Toronto, Toronto, Ontario.

J. McLintock
Canada Department of Agriculture, Research Branch, Saskatoon, Saskatchewan.

M.S. Mulla
Department of Entomology, College of Biological and Agricultural Sciences, University of California, Riverside, California, U.S.A.

C.E. Osgood
Canada Department of Agriculture, Research Branch, Winnipeg, Manitoba.

B.V. Peterson
Canada Department of Agriculture, Entomology Research Institute, Carling Avenue, Ottawa, Ontario.

G.O. Poinar, Jr.
Division of Entomology, College of Agricultural Sciences, University of California, Berkeley, California, U.S.A.

M.W. Provost
Entomological Research Center, Vero Beach, Florida, U.S.A.

A.M. Pucat
Champlain Regional College, St. Lambert, Quebec.

K.S. Rai
Vector Biology Laboratory, Department of Biology, University of Notre Dame, Indiana, U.S.A.

J.G. Saha
Canada Department of Agriculture, Research Branch, Saskatoon, Saskatchewan.

M.W. Service
Liverpool School of Tropical Medicine, Pembroke Place, Liverpool, England.

B.N. Smallman
Department of Biology, Queen's University, Kingston, Ontario.

K.M. Sommerman
Arctic Health Research Center, College, Alaska, U.S.A.

F.E. Strong
Department of Entomology, College of Agricultural and Environmental Sciences, University of California, Davis; California, U.S.A.

D.E. Weidhaas
Entomology Research Division, Agricultural Research Service, U.S. Department of Agriculture, Gainesville, Florida, U.S.A.

A.S. West
Department of Biology, Queen's University, Kingston, Ontario.

D.R. Whitehead
Department of Entomology, University of Alberta, Edmonton, Alberta.

PREFACE

The outstanding need for an assessment of the current state of our knowledge of biting fly control was formally expressed at a meeting of the Advisory Committee on Entomological Research to the Defence Research Board (ACER) held in June 1970. At this meeting the Committee confronted their terms of reference and recognized two major tasks arising from them: the first was to prepare a balanced program of basic and applied research in the field of medical entomology with emphasis on problems affecting the armed forces, and the second to assign priorities.

At the following meeting in November of the same year the Committee commenced preparation by listing subject areas of particular concern to the Department of National Defence and assigned priorities within them. Area control and the protection of individuals were recognized as the two main approaches to biting fly control, with better chemical agents and alternative methods comprising the main divisions of the first, and repellents and fundamental studies of the behaviour of biting flies being important components of the second.

The next step was to try to determine where we stand in respect to progress in all these areas, and it seemed most logical to ask this question of the people who are doing the work. The Committee decided that this could be done most effectively and rapidly by means of a symposium, and the conference reported in these Proceedings resulted directly from this decision.

The objective laid down for the symposium was that it should provide up to date information on the status of research on biting flies and recommend areas for research and development to which funds could most usefully be directed. The speakers were asked to define specific problems, discuss new ideas and methods, and to emphasize those which are feasible now, and to point out where intensified research could bring others within reach.

While arrangements for this meeting were in progress its potential range of influence was extended by a recommendation that the Department of Agriculture should assume responsibility for the coordination of research and control of biting flies in Canada. The additional function which the symposium could have in providing a background of information for program-planning by CDA was duly considered in the making of recommendations, and in formulating the resolutions.

The arrangement of the symposium program closely followed the subject areas identified by ACER in 1970. Area control was considered with respect to conventional and unconventional chemical methods and also with respect to biological control. The protection of individuals was considered under the headings of repellents and the behaviour of blood-feeding insects. Each group of papers was followed by a two-part discussion period, chaired by a discussion leader. In the first a group of two or more invited discussants took part, each of whom had received prior notice of the contents of the papers. The second section consisted of questions and discussion from the floor. These were extremely lively and useful periods and they are reported in this volume following the papers given on each of the three days. Each day ended with a summation of the deliberations given by one or two rapporteurs; these syntheses gave emphasis to the points most closely related to the objectives of the symposium and are reported at the end of each session.

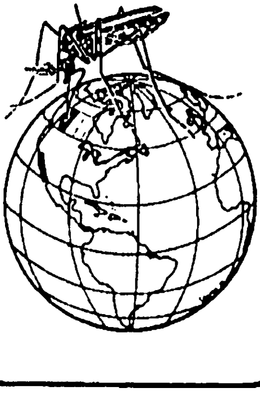
At the conclusion of the meetings an *ad hoc* committee consisting of the rapporteurs, two members of the Symposium Committee and one observer, drew up a series of resolutions which were presented to the meeting. These were discussed and modified in an open session and received overwhelming support, 78 being in favour, none against, and 5 abstained. The Resolutions Committee was empowered to make minor modifications of style, and the results of the exercise are included in this volume following the summary of the last section.

In his welcoming address the President of the University of Alberta, Dr. Wyman, said that in his opinion Canada was going through a cult of technology and innovation, and that this must eventually suffer the same fate as the cult of education and basic research which prevailed in the 1950's and 1960's. At present the Federal Government is spending enormous sums of money on improvements in technology, but this cannot last for it must be realized that advancing technology is not an end in itself. The world's problems cannot be solved without education and research, and we must hope for a rapid swing back in this direction if such matters do indeed follow a cyclical pattern.

A study of the contents of these Proceedings leaves no doubt of the need for the allocation of additional funds to biting fly research, and clear indications are given of the areas where these could most profitably be allocated. The preservation of environmental quality was everyone's grave concern and we can only do our best to see that this is communicated to those who can translate the recommendations into action.

Anne Hudson
Ottawa, 1972.

STATEMENT OF THE PROBLEM



ENVIRONMENTAL QUALITY AND THE CONTROL OF BITING FLIES

Maurice W. Provost
Entomological Research Center
Florida Division of Health
P. O. Box 520
Vero Beach, Florida 32960

> "Man is one of the many competing species in the world's interdependent fauna and his very existence is inextricably interwoven with that of the other animals in his environment."
>
> A. D. Pickett (1949, p. 67)

> "Man himself must be regarded as merely an important biotic part of the environment. He lives or works within it and, while so doing, profoundly influences not only his immediate surroundings but also the cohabitant fauna."
>
> G. C. Ullyett (1951, p. 460)

If I preface my remarks with quotations from two eminent Canadian entomologists, please don't think I'm trying to be ingratiating. These men expressed the gist of my talk, they did it almost a quarter century ago and while warning against the misuse of the new insecticides, and they happened to be Canadians at the time.

In seeking physical comfort Man reveals his animal nature and in wanting his life to have meaning he shows he's kindred to the angels, if this quaint allusion is still permissible. The duality may well be the essence of this symposium: animal man wants to control biting flies but spiritual man also wants environmental quality, and reconciliation becomes the order of our day. Biting flies and their control are a subject hardly in need of elementary description to this audience and they will receive expert attention in the next few days. But the expression "environmental quality" begs a definition. It is obvious that none will be found acceptable to all of us here. Yet the attempt at a definition must be made if we are to discourse at all. Quality can obviously be good or bad, but I'm sure we all understand that we are here talking of maintaining an environment of high quality. I hope my effort to define such an environment is not too arrogant or too idiosyncratic.

An environment of high quality will first of all assure the biological survival of man. Gross pollution of air, land, and water is posing a global threat to survival right now. Equally threatening is the rapid depletion of non-renewable resources which will be as critically needed by man generations hence as they are now. And, finally, the biological survival of man will demand an environment containing lesser numbers of Man himself.

In addition to assuring the survival of mankind, an environment of high quality will provide man with surroundings which are adequate to his spiritual nature, by which I mean an esthetically and culturally satisfying environment. Philosophers and historians of art have disputed endlessly on the meaning of beauty, yet every man, learned or not, knows that beauty exists and that only man, among animals, can conceive it. It is a sort of instinct of the mind for the fitness of things, as essential as any instinct of the body, for without beauty in his environment man's behavior becomes bestial and he no longer functions as *Homo sapiens*. In much the same fashion, culture is an essential component of man's environment. Broadly conceived, culture is heritage, or the mementos of one generation to another. Everyone knows that communication across the generations was the beginning and remains the *sine qua non* of civilization. So whatever is done to the environment should not erase the least of the worthwhile monuments of the past.

One quality of the environment which should be maintained at all costs is diversity, for in the biota it promotes that biological stability without which chaos is forever imminent while in the landscape it satisfies man's innate desire for interest, beauty, and peace of mind. The biosphere is diverse beyond comprehension and it must remain so if any component of it, including man, is to survive.

I. The Environmental Crisis

Everything has its environment, but in today's vernacular *the* environment is the biosphere. It is the surface of the earth conceived as a substrate for life or as a support system for a vast number of interacting and interdependent forms of life, including man. This environment has changed immensely during the six billion years of its existence and considerably even during the one million years of man's occupancy. But over short periods the planet's surface has a certain degree of homeostasis. Because it also has resiliency, man has been able to modify it. In recent decades this modification has been catapulted into widespread destruction (Commoner, 1971; Caldwell, 1972), hence the environmental crisis. Hence also next month's United Nations Conference on the Human Environment, to be held in Stockholm. That conference will be a fitting culmination for the three most significant decades in the history of the human species.

One might characterize the last three decades in this manner. The Forties were the War Decade. In the first half of that decade mankind waged war on itself. In the second half of the forties war was declared against man's environment. Nearly all elements of the present crisis began their major escalation in those late forties. The new technology was born, the lamentable one which today holds the overdeveloped world in a death grip. This was the "sweeping transformation of productive technology" whereby "technologies with immense impacts on the environment displaced less destructive ones." (Commoner, 1971).

The Fifties were the Sleeping Decade. People were luxuriating in suffocating complacency and blissful ignorance. The environment was deteriorating at a fearsome rate, but the gross national product was climbing every year so God had to be in his heaven and all had to be right with the world. The few and well scattered voices crying in the wilderness were drowned by the decibels of humming industry and economy. Consumerism and escapism ruled the day.

The Sixties were the Waking Decade. Although many had spoken before, the voice first heard widely was that of Rachel Carson. Her "Silent Spring" (1962) caused no less than a furore, and although it ushered in a virtual explosion of books about the suffering environment, the treatment accorded that first trumpet call is still the fate of even the most recent books. The best-informed and least impassioned writers on the subject are still called scare-mongers, doomsayers, disaster lobbyists and worse, – usually, as David Brower (1971) points out "by those who profit from apathy and from postponement of the day of reckoning." But the cry was heard nevertheless and by the end of the decade demonstrations, congresses, television shows, and other means of expression joined a fabulous proliferation of books depicting the environmental crisis, as everyone called it by then.

The Seventies have started with a truly global concern over the problem. New journals devoted to the environment and its problems are sprouting all over the world. Books with more sophistication and better documentation, and therefore more convincing, are coming off the presses. It should not take many more such books as Barry Commoner's "The Closing Circle" to convert even the most ordinary man on the street to the need for fast and drastic action. And no one has better characterized the environmental crisis and its belittlers than Lynton Caldwell (1972) in his excellent book just off the press *In* Defense of Earth: "Under the slogans 'progress', 'development', and 'economic growth', the policymakers of modern times have proceeded to reshape the world with only the slightest regard for the ultimate consequences of their actions. And, when confronted by the evidence of damage to the life-supporting base of modern society, a large and influential number reject the data as emotionally biased, exaggerated, or insignificant."

The true meaning of next month's United Nations Conference on the Human Environment is that for the first time the global nature of the environmental crisis will be universally recognized. Probably the two greatest elements of crisis (there are many others) are pollution and depletion of natural resources. Consider the international complications in these two only. Not only are nations plundering each other's natural resources but the overdeveloped countries are polluting the air, water and food of other countries as well as their own. The secretary-general of the conference, Mr. Maurice F. Strong, predicted in an interview (1972) that "Environmental aggression will become a dominant factor in the affairs of nations."

II. Biting Flies and Environments

It is extremely appropriate that a discussion of environmental quality and the control of biting flies should take place in Canada. No other country, with the possible exception of the Soviet Union, presents such an environmental spectrum from the ultimate in metropolitan habitats to the most uninhabitable expanses of wilderness. No other country presents so dramatically the full span of human density, from urban masses to rural dispersions and from frontier communities to outpost domiciles. And to complete the picture, for all these disparate environments and human densities there are populations of biting flies much in need of control.

Both biting flies and environments can be classified in an artificial manner and discussed individually in partial vacuums, i.e. as though man did not exist. Our concern with environmental *quality*, however, makes it clear that the human element must enter the consideration. Modern geographers have done a beautiful job of integrating physiography, ecology, and sociology; and no better example of this can be found than the Centennial commemorative volume prepared by the Canadian Association of Geographers entitled "Canada: A Geographical Interpretation" (Warkentin, 1968). This book very sensibly describes the country under seven regions: The Atlantic Region, Southern Quebec, Southern Ontario, The Prairie Region, The Canadian Cordillera, The Forest Frontier or Subarctic, and The Arctic. Physiographically and ecologically the first five regions can be conceived as extending southward into the United States, so it is not surprising that biologists in both countries have long studied the biting flies they contain and the annoyance problem they pose. The Subarctic and Arctic Regions, however, except for small montane oases, are unique to Canada and Alaska in this hemisphere. Their biting flies were not studied very much before World War II. Immediately after the war, the Defence Research Board, recognizing the fast-growing military value and economic exploitation of the far north, requested and supported extensive studies of northern biting flies and their control (Hocking, 1952; Twinn, 1952). It was early established that in the arctic, mosquitoes are the major biting fly, with black flies producing much less annoyance. In the subarctic, however, mosquitoes are not only a tremendous annoyance but are joined by black flies and tabanids in horrendous numbers.

For the purpose of our symposium, the environment and its biting flies could be broken down further into natural habitats. This, especially for Canada, would be a book-sized task and would furthermore not subserve our purpose of talking about quality in the environment. Suffice it to say that every type of terrain, – mountain, prairie, tundra, floodplain, etc. – has its own variety of surface waters and that each of these waters produces certain kinds of mosquitoes. Also most flowing waters produce black flies and nearly all wet soils produce horseflies and biting midges, the big and the small among biting flies.

III. Encounters with Environmental Quality

Man encounters biting flies in a multitude of environments. He may share his house or his farm buildings with them, they may annoy him as he goes about his work in fields or woods, they may frustrate his every effort at outdoor recreation. There are still many parts of the world where at certain times of the year biting flies make life for man unbearable without protection, if not impossible. This is the case in the arctic and subarctic of Canada (Defence Research Board, 1965; Hocking, 1952), and below, in the boreal forest. However, the biggest global impact of biting flies on man has been, of course, in the dissemination of disease; and for this purpose it is not necessary that the bite be annoying. Although diseases vectored by biting flies have never been very consequential in Canada, the country has nevertheless supported excellent researches in medical and veterinary entomology. Biting flies in Canada are overwhelmingly an annoyance problem. And if we are now to target in on the matter of how the control of these pests impinges on environmental quality, we could do it best by following man in his activities and the annoyances he is encountering and combating.

Home Environment

Quality in a home environment is a pretty personal matter and not likely to be affected by controlling biting flies unless the flower vases hold water and breed *Aedes aegypti*, – which wouldn't happen in Canada.

Residual spraying the interior of homes, whether it's to eliminate disease-carrying insects or just plain pests, can't do anything but improve the quality of a home environment. My most vivid memories of malaria-control days in Florida are of the morning-after inspections of so many of the humble shacks we sprayed with DDT. The poor housewife often enough would come to me with tears of joy and show me a basketful of dead bedbugs, roaches, and other vermin, and she would exclaim that her family had spent the first night of their lives without annoyance from biting or creeping things. I'm sure these sentiments are no different than those of millions of people throughout the tropics who have experienced residual spraying of their homes for the control of malaria, leishmaniasis, Chagas' disease, or other vector-borne illnesses. I sincerely hope that those who would restrain the use of DDT will remember that, used in this manner, this insecticide not only is harmless ecologically but it actually enhances environmental quality no matter how construed.

Premise Environment

The immediate surroundings of a home can be anything from gardens and patios to barnyards or the remains of the wild bush. If not properly maintained they can readily enough produce biting annoyances. Domestic mosquitoes, *Culex pipiens*, come to mind first. Any standing water, no matter how polluted, will breed these. Control is achieved by simply eliminating such waters, or if not permissible, screening them.

In the tropics other mosquitoes, including malaria vectors, may be primarily premise-breeding problems. Indeed, the great majority of disease vectors live and breed in very close association with man's domiciles. Being domesticated or semi-domesticated, those biting flies which originate on home premises are usually controlled through good sanitation alone, – an unfailing way to improve environmental quality.

Urban Environment

Although city-dwellers may be bitten by mosquitoes and other biting flies flying in from long distances, as is the case right here in Edmonton, more often than not the biting annoyances are produced right there in the city. Superimposed on possible production on private premises, biting flies may arise from a number of public facilities, usually for drainage or sanitation. *Culex pipiens* is usually the culprit, which is why a sanitary engineer may be in charge of abatement as often as an entomologist. Open ditches, park lakes and pools, and other such public waters may produce many other kinds of biting flies, and in nearly all cases keeping these waters clean will prevent breeding. This should be a matter of civic pride.

Rural Environment

Millions of urbanites in the overdeveloped countries live under the illusion that they are completely emancipated from Nature. By contrast, rural peoples traditionally and in reality feel closer to Nature. Virtually throughout the world they are annoyed by biting flies, and they generally know where these arise. Manipulating soil and water is at the heart of farming, so whether it's rice paddies in Indo-China or irrigated alfalfa here in Alberta whoever farms is in a position to create many biting-fly problems unknowingly and certainly unwillingly. We are now talking about more than mosquitoes. Ditches can produce black flies in abundance on the Canadian prairie, for instance, and wet or soggy pastures, or parts thereof, can produce tabanids and ceratopogonids, i.e horseflies and biting midges.

In almost every case where investigations have come up with a solution to a biting-fly breeding situation on farmlands or ranchlands, that solution has been a general improvement in agronomy or range management. There are therefore several inducements to farming or ranching without producing biting flies. If, however, the breeding problem cannot be resolved culturally or engineeringly, then those methods to be discussed for the wild environment must be resorted to.

Wild Environment

Throughout the world and most especially in Canada the great biting fly annoyances are produced on the land at large and their control must be a community or governmental effort. The tidelands of the maritime provinces produce mosquito and tabanid swarms while the country's Pacific salt marshes yield mosquitoes and biting midges. River plains produce hordes of mosquitoes after freshets, while the streams themselves, even to the smallest rivulets, produce black flies. Forests, from border to tundra, produce flood-water mosquitoes in their temporary pools, – which are legion. The tundra is notorious for its snow-melt mosquitoes. Unsettled mountains, plains or prairies all produce an abundance of biting flies to greet the worker or vacationer.

Everyone knows that water is just about everywhere in Canada in the warmer months. How much surface water and muskeg is there in the million and a half square miles of taiga and tundra on the Shield and around its edges? This water serves a purpose in Nature's economy. Yet this is the water which produces all those mosquitoes, moose flies, deer flies, no-see-ums, etc. and none of it could be drained without great environmental damage, – even were it possible. Therefore what is usually called source reduction or "permanent control" is an impossibility for the biting flies on Canada's wild terrain. This leaves temporary control, which is the use of insecticides, as the only possibility of relief, excluding personal protection.

Starting with DDT, organic insecticides have run the gamut from boon to mankind to pollution of the earth. There is a reason for this and it is tragic. Possessed of a miraculous tool in DDT and disregarding numerous warnings, men proceeded to use it recklessly, killing pests and their natural enemies together, and generally ignoring the biosphere and man's place in it. Nature responded by counterbalancing unilateral chemical programs with the enormous fitness of insects, – they became resistant to the chemicals. Insect damage to food, fiber, and forest products today is not a bit less than it was before the advent of DDT, – we have nothing to show for having polluted the earth and its oceans. And the control of biting flies with DDT and its descendants was not blameless either. One could enumerate program after program against biting flies which was ill-advised, self-defeating in the long run, and damaging to the environment. But this would serve no purpose at this time. Rather we need to give positive attention to our use of insecticides against biting flies.

In Canada's arctic and subarctic regions, particularly, but also elsewhere, there are innumerable frontier setttlements and outposts, not to mention military facilities, where, without equivocation, man simply must be protected against biting flies. Personal protection methods are enormously improved over what they were before World War II, but it is the opinion of most experts that more is needed, and this more has to be larviciding and space spraying of adults. Fortunately there have appeared lately some candidate insecticides which appear to be very innocuous against non-target forms of life at dosages effective against biting flies, particularly mosquitoes and black flies. Every effort should be made to promote both research and use of these, while looking for more and better pesticides.

No environment places Man within the biosphere so unquestioningly as the wilderness. This is so not only in the sense of satisfying esthetic cravings but in a very real, physical sense. I can think of no better way for a man to become corporeally united to the biosphere than to have his blood scattered over the landscape in the form of eggs from a thousand flies. And Man can really feel his affinity to the moose and the caribou when he is pursued and attacked by swarms of mosquitoes, black flies, and tabanids.

IV. Conclusion

One hears a lot about revolutionary new methods of pest control since insecticides have fallen into so much disrepute in many quarters. Biological control itself is not new, especially the use of predators and parasites, but the deliberate propagation of insect diseases is quite recent. The possibilities residing in growth hormone simulators are receiving considerable attention. Genetic control methods offer probably the most environmentally considerate methodology. However, all these new methods have one thing in common. They will require for successful use, or even development, a far more sophisticated knowledge of the biting flies than we have now, especially in the areas of behavior and ecology.

Speaking of ecology brings to mind Aldo Leopold pleading for men to love and respect the land. In a widely distributed essay (originally speech), Ian McHarg (1971) made this statement about the United States: "Two hundred million people who don't know enough to insure our survival, and probably only 200 ecologists who know that which everybody should know." But Leopold, himself an excellent ecologist, had this to say many years ago (1949) to those who see salvation coming only from professional ecologists: "Let no man jump to the conclusion that Babbitt must take his Ph.D. in ecology before he can 'see' his country. On the contrary, the Ph.D. may become as callous as an undertaker to the mysteries at which he officiates." Indeed, the concept of the biosphere, which is the key to understanding man's place on earth, originated with the French naturalist Jean Baptiste Lamarck, the word was first used by the Austrian geologist Edward Suess, was developed into its present usage by the Russian mineralogist V. I. Vernadsky, and was popularized by the French priest and paleontologist Pierre Teilhard de Chardin (*cf.* Caldwell, 1972). I mention this not to detract from ecology but rather to emphasize that the science of the environment cannot overcome the present crisis, – only the ethics of the environment can help now, and they are social and political.

However much Man is bound to the biosphere, the biosphere is too distant a concept for the average person to empathize with. "Love thy neighbor" reaches how far? Across the seas to the alien Chinese? Where is the evidence? Across the ages to our children of a thousand years from now? Who can believe it? Aldo Leopold (*opus cit.*) pleaded eloquently for a *land ethic* based on love. From "love thy neighbor," in effect, we must go on to "love thy land." But 25 years later people still have not learned to love the land. And now things have reached a state where we clearly need an *Earth ethic*: "Love thy planet." But as long as things and land and Earth are all equally treated as simply commodities, there is little hope for their respectful and loving care. If we find it hard to love our unseen brethren across the globe or across the ages, how can we love the million times more remote forms of life, many invisible to the naked eye, which together with us form the biosphere? How many Teilhard de Chardins can there be among our 3½ billion?

A few years ago, I was so irritated by insinuations in the liberal press that environmental concern was just a preoccupation of the affluent that I wrote strong letters to the editors of several journals reminding them that the impending ecological disasters would hurt or kill the poor as well as the rich. One typical article entitled Pollution and the Poor: The Coalition of the Clean ended on this note (Barthelmes, 1970): "it is hoped that the human spirit will be cleansed, – after that, the air and water." If a supposedly learned man can think in this way, what can we expect of the multitude? Raymond Dassman (1968) gave the frightening answer: "You cannot talk of nature to somebody who has seen it only in a city dump . . . . When the millions in Calcutta cry out to preserve the wild Himalayas, when Harlem votes to preserve the grizzly bear, the battle for the human environment will be won."

The rational in me tells me this may well be so, and it also tells me that if it is we are doomed to early extinction. But someone said a grandfather can't be a pessimist, so I try not to be one. I prefer to believe that the battle for the human environment will be won if only those privileged to fight it do each their part, be it large or small. In the light of the world's plight, ours here is not really a staggering demand. In doing a very humane thing, protecting people from the torture of biting flies, certainly we can do it in a manner also humanitarian, -- by preserving environmental quality as much as we can. I say humanitarian because, as Caldwell (*opus cit.*) has so well put it: "Cynics rightly say that the world could struggle along without the pelican or the whooping crane; they do not often note that it could as easily do without man."

And, finally, as for being optimistic in rather somber circumstances I feel very much as the man who wrote (Ross, 1971): "Doomwatchers we have now aplenty, all the way from the Massachusetts Institute of Technology and the World Bank to the front pages of the popular press; Doomchallengers are much, much thinner on the ground." So let's all be doomchallengers.

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ENVIRONMENTAL QUALITY AND BITING FLY CONTROL: PROBLEMS AND POSSIBILITIES

Brian Hocking
Department of Entomology
University of Alberta
Edmonton, Alberta

There are terms in my title which are open to various interpretations. I propose therefore to give you my definitions of them. Many would equate environmental quality with clean air, clean water, and clean soil, which is a good starting point. But how clean? Clean enough for you and me? Or clean enough for a multiplicity of plant and animal species? I think the latter, and not merely for sentimental or even aesthetic reasons, but from hard-nosed, practical considerations. For over a century of practical pest-control experience reinforces the evidence from both population theory and ecological research and experiment to the same end, namely that diversity spells stability. Stable populations raise no problems; save perhaps, of people, for conservative economists. What is good enough for us may not be good enough for our food chains. It is important to distinguish between standard of living, which is related to gross national product, dimensions of television screens, and numbers and horsepower of automobiles, and quality of life, which is indefinable but related to environmental quality as I have defined it. Beccario's dictum: "the greatest good of the greatest number" is meaningful today only if we are speaking of numbers of species, not of people. Is this standard of environmental quality compatible with the control of biting flies? I hope to show that it can be, although I have been instructed to confront the possibility that I am wrong.

None of the insects we are concerned with are, technically *biting* flies: no adult flies, certainly not the horseflies, blackflies, or mosquitoes, have what entomologists call biting mouthparts. But it is a hopeful sign that we have seen fit to use this term in our title, for the layman sure as hell gets bitten by them. And one of the problems I shall refer to concerns communication with the layman.

The meaning of control is unequivocal to the layman. It is sad that among entomologists, for some 30 years, it has often been hard to discriminate between the words "control" and "kill". There are hopeful signs of change, that is, of a return to say pre 1940 usage. When I first studied applied entomology, well before 1940, believe it or not, I was taught to control not insects, but outbreaks, and to control them by discovering and undermining their causes. Insecticides were billed as a first aid measure only, to keep the customer quiet while an entomologist got to work on the underlying causes. We were warned by our mentors against condoning the continuing use of a poison. When our layman kills the motor in the car he drives he does not consider that he is controlling it. It is in the layman's sense, again I think appropriately, that I shall interpret the word 'control' in our title.

Problems

During the winter of 1946-47, Alec Jones, a textile technologist on the staff of the DRB in Ottawa, with whom I had previously worked in India, stirred up interest in the biting fly problem at Churchill, Manitoba. In 1947 – a summer to remember – with a contingent from the east, another of Americans, and a flying visit of a group from Suffield, Alberta, we came up with successful recommendations for the first aid control of, at least, mosquitoes and blackflies which, with minor changes, have been followed at northern bases ever since (Defence Research Board, Symposium, December 15-17, 1948). Perhaps they were too successful, for we had no sooner got our teeth well into the underlying causes, with a laboratory and a field station established at Churchill, facilities at Goose Bay in Labrador and Whitehorse in the Yukon, and mobile parties elsewhere in the north, when funds began to dry up. The laboratory at Churchill, and even that at Suffield were closed down. Most of us were doing this work on a part-time basis and had full-time jobs elsewhere. We protested but doubtless less vehemently than had our livelihoods depended on it. The appointment of several full-time entomologists to advise the armed forces on current practices and new developments was urged; one such appointment was made, in the Surgeon-General's office, to provide training for service personnel and continuing supervision of the biting fly and all other insect control operations, in all branches of the armed forces. Research dwindled to minor part-time projects at Universities, with initiative resting largely with University teachers, through an advisory committee. It can only be supposed that those in authority thought the problems were all solved; certainly the attempts of those who knew otherwise to disillusion them failed.

To get down to specific examples: firstly in the realm of personal protection. In 1948 a number of insect-proof suits -- empirical prototypes designed by Jones – were tested in the field at Churchill; reports were written on their good and bad features. Other ideas on protective clothing came out of the reports and from elsewhere; in 1952 (Hocking, 1952a) for example I extended some work of Davies (1951) and discovered that among several tested, air force blue was by far the most attractive fabric to blackflies; two and a half times as attractive as khaki drill. Since the attractiveness of this fabric to blackflies rests largely on its ultra-violet reflectance, it can be changed without upsetting the colour sensitivities of the Royal Canadian Air Force. The air force still complains about blackflies, and Canadian forces still have no protective clothing designed for northern fly-time.

At a Defence Research Board Symposium in 1948, Kingscote reported a solid preliminary study on oral administration of biting fly repellents. While his results were mostly negative his report ended on a hopeful note, but this subject too was allowed to drop until 1962 when the Surgeon-General's branch of the U.S. Army re-opened it and wisely channelled part of the available funds into more basic aspects of this problem. It has been our pleasure and privilege at the University of Alberta to be involved in this work.

In 1956 a large scale experiment with air dispersal of DDT impregnated bentonite granules against mosquito larvae was conducted at Namao, northeast of Edmonton. DRB, RCAF, the University of Alberta and the City of Edmonton co-operated -- a hopeful sign. This showed that satisfactory mortality could be obtained with one-tenth of the amount of DDT per acre required for application in oil solution. This technique was adopted in the same year by the City of Edmonton in its mosquito control operations, but I believe has not been generally adopted elsewhere and certainly not by the Canadian armed forces. If it had been, perhaps the useful life of DDT would have been extended tenfold.

Last year we had an unusual population of *blackflies* in the SW quarter of the city of Edmonton in the spring and many children required hospital treatment for their bites. This spring medical practitioners are urging improved *mosquito* control saying "many people don't appreciate the disease and allergy problems resulting from such pests". Clearly, medical practitioners must be included among these "many people"; but equally clearly it is our fault as much as theirs.

A year ago a sub-committee of the Defence Research Board Advisory Committee on Entomological Research made a convincing case for the appointment of several additional full-time staff with entomological qualifications to work with branches of the armed forces and assist in ensuring the prompt and coherent application of the results of research, to their immediate benefit. Shortly thereafter, despite representation from the advisory committee, the one existing appointment was terminated.

The need for development of new aerial application techniques -- one of the possible routes to greater specificity – has long been apparent; yet experimental aircraft have not been forthcoming.

All of these problems seem to me to have at least two causal elements in common. Firstly our knowledge of entomology, as well as that of some related disciplines, is clearly inadequate to the task before us. But even clearer is the problem of communication; our own ignorance as entomologists is shameful enough, but that greater ignorance in which we have left so many people, both the general public who ultimately pay the bills and especially the many many people who find themselves, often against their better judgement, doing entomological jobs, presents I think, a more pressing problem.

We must communicate -- for our own salvation -- widely and deeply, in words of two syllables, one syllable, and on occasion four letters. The current anti-education wave makes this no easier, but perhaps we have brought this upon ourselves. We as entomologists cannot do this alone -- we are too few in the rising tide of people -- but we must get chain reactions or pyramid selling, or whatever the phrase of the moment may be, to help us. I see more and better biology in the schools and more and better entomology in biology as primary targets. The privilege of learning carries with it a responsibility to teach: and not merely a conveniently small class in an ivory tower. The governing body of the Entomological Society of Canada has a proposal before it which is a step in the right direction. We hope some more steps will be proposed at our second symposium on Friday.

Possibilities

There are two possible approaches to biting fly control, the fly population reduction approach by biocides or biologically, and the personal protection approach. The former is already capable, locally and in the short run, of meeting most people's standards of biting-fly control and perhaps -- in a much shorter run however -- many people's standards of environmental quality. But in my view, extensive long-term control with the standard of environmental quality which I have set forth is generations away. The latter, personal protection, as yet the subject of a rather small volume of rather inexpensive empirical research, already meets my personal standards of control (though admittedly it falls far short for many other people) and is virtually free of environmental threat.

Let us examine the possibility of population reduction.

Over the greater part of the land area of the earth one or several of the main groups of biting flies are to be found abundantly represented in terms of species and of individuals, and ubiquitously disposed. The great majority of them are dependent on two fluids, the nectar of flowering plants and the blood of vertebrates. These essential links with the two major groups of organisms of direct interest to man must surely mean that the extensive removal of biting flies -- even if it were possible and however it might be accomplished -- would of itself have far reaching effects which as yet we can only guess at. Truly extensive removal is being talked of; in Alberta a "province-wide (mosquito) control program" -- some quarter of a million square miles. Of course there are good arguments for large scale operations, notably the remarkable "flight" range of many species; the record for mosquitoes stood for many years at 110 miles -- at sea off Cape Hatteras (Curry, in Matheson, 1944) but Asahina and Turuoka (1968) have recently extended this to 310 miles (500 km) in the Pacific.

What insecticides would be used in such a project? Nothing presently available has the desirable biochemical specificity; few effective compounds degrade at a desirable rate, to known innocuous products. Hormones -- "juvenoids" and their allies -- are in view but their specificity and safety are questionable and they have a remarkable backfire potential. Perhaps all we can hope for is specificity of application techniques -- probably part of the explanation of the success of bentonite granules. In this, of course, aircraft represent a backward step in relation to ground application -- until we can recognize larvae from a helicopter. Further progress demands a better understanding of feeding behaviour and ingestion (Chance, 1970; Pučat, 1965).

It is worth noting that our predatory chaoborine larvae are more susceptible to many of our insecticides than the larvae of the pest species they prey on; even an insecticide that is family specific would thus have a significant mark against it. Industry gives us terrifying figures on the cost of developing a new insecticide and indicates that specific compounds to control specific insects cannot be an economic proposition. All things considered the technology which would allow insecticidal control of biting flies as extensively as is contemplated, along with maintenance of environmental quality, seems too far in the future to make guessing, at either a date or a cost, worthwhile.

What about biological, in the broad sense, including genetic control? Some hopeful approaches will doubtless be mentioned by later speakers in this symposium – but I doubt whether anybody will be so bold as to put a date on the successful use of any of these methods for extensive control in northern Canada. It is perhaps necessary to mention that biological methods of control can have no less disastrous effects on the environment than chemical methods, although this is much less likely to happen.

There remains of course the integrated approach. Some of the problems in this may be illustrated by the story of the purple martin, *Progne subis*. Some years ago an enterprising American manufacturer of bird nesting boxes advertised widely, if unwisely, the value of these birds in mosquito control. They are a valuable component of the environment in their own right and there has been a phenomenal increase in nesting boxes in Edmonton as in many other cities. Occupancy is high but reproductive success is low, nestlings usually dying during inclement weather, it seems from a shortage of food (Boag, 1972; Lister, 1972). Two independent bits of evidence reinforce each other to show that death is not due, however, to a shortage of mosquitoes. Firstly, these insects have been peculiarly abundant during the last few years in Edmonton. Secondly, studies at Elk Island National Park have shown that mosquitoes, though also abundant there, do not contribute materially to the diet of purple martin nestlings (Spice, 1972). Two other insects of aquatic origin however do: dragonflies and the dronefly *Eristalis tenax*; their populations must be reduced by mosquito larval control with insecticides, and dragonflies are of moderate importance as predators on adult mosquitoes in this area (Pritchard 1963).

If we really want extensive population reduction of the three major groups of biting flies it will certainly take many years to achieve. It will take money as well as time: laboratories at strategic locations in the north; many full time permanent research staff with appropriate facilities, equipment and supporting staff for continuous biological and chemical monitoring; well qualified extension biologists to ensure that civilian and military operations conform to specifications. It cannot be done with a handful of part-time help.

What are the possibilities of success through the personal protection approach? Most of the items used to protect man and other animals from biting flies have come into use through testing of existing items, usually developed for other purposes. This is true of nearly all skin and clothing repellents, developed for various purposes; of fabrics and clothing made from them, developed for wind proofness; of fly-proof buildings for shelter or for advertising (Hocking, 1960); of nets and screening for fishing, beekeeping etc.; even of the familiar yellow lamps, supposedly insect repellent. Despite the fact that the basic knowledge of spectral sensitivity of the eyes of both man and insects was available, so that any sensory physiologist could have designed such a lamp, lamp manufacturers developed them by tedious empirical testing. This, and the fact that the still more familiar window screening is still almost invariably woven and installed the wrong way up (with the long axis of the mesh the same way up as the long axis of a mosquito in normal resting attitude) is further evidence of the communication problem.

How much better could we do if, firstly, we had a full understanding of the sensory physiology and behaviour – especially the blood feeding behaviour – of all groups of biting flies, and, secondly, if we went to work on a program of redesign and scientific testing of all of these items based on this understanding. Anybody who professes faith in science, must assuredly answer: one hell of a lot better! Such a program too would cost time and money, but of a different order of magnitude to the costs for a program to reduce populations. I would even hazard a guess that after ten years work by two closely collaborating establishments, one on the physiology and behaviour and the other on the design and testing of products, we would have a collection of items that would keep almost everybody happy in the most severe fly-conditions that northern Canada – or any other place – has to offer. Again, of course, full-time staff would be needed.

There are a few special points worth mentioning: distance piece clothing has not been widely used, perhaps because it is cumbersome. Modern technology would allow the incorporation of the distance piece principle into a single lighter, more convenient fabric. Although the lengths of the proboscides of most mosquitoes are in the taxonomic literature, nobody, I believe, has studied the relationship between these lengths, and the *effective* reaches of mosquitoes through fabrics.

The reluctance of people who contentedly spray lethal chemicals over their immediate environment to rub a little of an innocuous repellent chemical over their own skins is strange and might be worthy of the attention of a psychologist. I listed other aspects of personal protection needing attention in 1952 and they still need attention, though some further work has been done on screening (Hocking, 1968).

What of the influence of such a program on the environment? Resistance to controls of this type is far less likely to develop than to insecticides, because of their many facets; they would seem likely to select for zoophilic habits so that researchers in this area would do well to bear in mind the possible need for livestock as well as personal protection. They could reduce populations. The possibility of protection of modest areas by spraying repellents on surrounding vegetation has been discussed from time to time but little work has been done on it; this possibility should be borne in mind in the development of new materials. The methods in general are virtually free of necessary environmental hazard. I believe that in this way, and perhaps only in this way, we can control biting flies and keep air, water, and soil clean enough for a multiplicity of plant and animal species.

Van Handel (1962) has drawn attention to the fact that the increase in coronary thrombosis as a cause of death in North America, and perhaps elsewhere, has taken place at the same time as increasing attempts at the control of biting flies. He suggests that the bites of flies may, by anticoagulants donated in exchange for the blood taken, have protected us from this disease. Since one of North America's malaria mosquitoes is singularly generous with this enzyme (Gooding, 1972), we have perhaps merely exchanged malaria for coronary thrombosis, a rather indifferent bargain! Whether or not this can be substantiated, it is a comforting thought to take with you into the bush this summer.

In Canada then, the collective mouths of better than a hundred and twenty species of blood-sucking flies rarely deliver, in payment for the blood they take, anything more than a possible antidote for coronary thrombosis. In many developing countries, crowded with undernourished humanity, every alternate biter may leave behind it an inoculum of malaria or any one of a dozen other dismal diseases. If the amount of toxic chemicals the world environment can accept is limited, as most of us I think believe it must be, the priority is obvious. William Cullen Bryant voiced a similar thought in reverse when he urged mosquitoes, instead of feeding on "gaunt poets" to:

> "Try some plump alderman, and suck the blood
> Enriched by generous wine and costly meat;
> On well-filled skins, sleek as thy native mud,
> Fix thy light pump and press thy freckled feet.
> Go to the men for whom, in ocean's halls
> The oyster breeds, and the green turtle sprawls."

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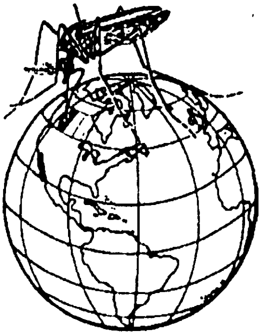
AREA CONTROL

Conventional Chemical Control
Unconventional Chemical Control
Monitoring and Assessment
Biological Control



RECENT CANADIAN DEVELOPMENTS IN AREA CHEMICAL CONTROL OF BITING FLIES

A. S. West
Queen's University
Kingston, Ontario

INTRODUCTION

This paper deals primarily with studies with which I have been associated, in the vicinity of Baie Comeau, Quebec, during the past seven years. Most of these studies were concerned with blackflies; mosquitoes received a minor amount of attention.

The modern period of area chemical control of biting flies in Canada began in the immediate post-World War II period with the availability of DDT. Experimental studies and practical control operations were conducted at Goose Bay, Labrador; Churchill, Manitoba; Whitehorse, Yukon; and elsewhere. This work was sponsored by the Defence Research Board of Canada and Canada Agriculture. There was a significant cooperative input from the U.S. Department of Agriculture and the U.S. Armed Forces.

Control techniques which were established became standard for a period of years, with relatively minor changes. Most airspray techniques were developed with fixed-wing aircraft; limited use was made of helicopters.

For area control of mosquito and blackfly larvae or adults it was established that, using several types of airspray equipment (straight emission pipe, rotary brush, boom and nozzle), a 200-yard swath width could be obtained when flying height was adjusted according to cross-wind speed. A height (ft.) X wind (m.p.h.) product of 600 was the basis of operation.

The DDT dosage for larviciding and adulticiding became established at 0.2 lb/a, and a preference for adulticiding over larviciding was common. For both types of operations blanket coverage of an area was the rule.

Control procedures against adult biting flies by the use of thermal-aerosol (fogging) machines were established. The recommended emission rate (or more accurately stated as input to the machine rate) was 0.28 lb DDT/100 yd front (5 lb/mi front).

During the fifties advances in mosquito control techniques included such developments as the use of lindane barrier swaths across a river valley to interrupt the migration of mosquitoes into the City of Edmonton, and the use of granular formulations of DDT, applied during the winter months, for the control of mosquito larvae (Winnipeg).

During 1953-1956 a major study of the biology and control of biting flies was mounted as a cooperative effort of Canada Agriculture, DRB, and the Pulp and Paper Research Institute of Canada. In 1953 the study area was in the vicinity of Des Joachims on the Ottawa River. Thereafter the base of operations was in the vicinity of the Baie Comeau, Quebec.

An experiment in control of blackfly larvae by air-spraying the perimeter of a drainage basin was unsuccessful because too many streams took their origin well within the perimeter. Blanket coverage (0.2 lb DDT/a) established that adult blackfly populations within a larvicided area would remain significantly below those outside the spray area for the entire season.

The 1957-1965 period saw a major increase in the use of airsprays for blackfly control in eastern Canada, particularly in the pulp and paper, iron mining and hydro-electric development areas of the Quebec North Shore and Labrador. When funds permitted, a larviciding and an adulticiding airspray commonly were requisitioned. If only one spray could be financed, the choice tended to be for adulticiding.

Low Dosage Blackfly Larviciding

The first major change in air-spray programs occurred in 1964, when 'low dosage' was introduced for the control of blackfly larvae. This procedure had been developed in New York State by Dr. H. Jamnback, and was successfully adopted in Canada without experimental trials. This technique involves flight lines at ¼ mi intervals, with the lines plotted to cross as many streams as many times as practical. Since 200-yd swaths still are obtained, less than ½ the overall area receives insecticide. As compared with a blanket coverage with a dosage of 0.2 lb DDT/a, the 'low dosage' procedure uses a dosage of 0.027 lb DDT/treated acre (or latterly 0.02 lb Methoxychlor/treated acre).

Gradually the 'low dosage' application came to be accepted, and there has been a reduction of single adulticiding air-sprays in favour of two larviciding sprays over a greater area, for a lower total cost.

Experimental Studies

During the summers of 1966-1971 a research centre was operated under my supervision, at Baie Comeau, Quebec. Studies were financed by DRB, WHO, insecticide manufacturers, municipalities, and pulp and paper, iron mining and hydro-electric companies. Studies on DDT-replacement compounds as blackfly larvicides formed the basis of an unpublished M.Sc. thesis by R.R. Wallace (Wallace, 1971); studies on particulate formulations of blackfly larvicides have been reported in an M.Sc. thesis submitted by B.V. Helson (Helson, 1972).

A. **Blackfly Control Studies**

The mounting evidence against DDT dictated an evaluation of other materials for chemical control of blackflies.

1. Larviciding

Oil formulations of six insecticides (Methoxychlor, Abate, Dursban, Cidial, Gardona and Fenitrothion) were tested for effectiveness as blackfly larvicides in both stream treatments on the ground and by experimental airsprays, and were compared with DDT as a standard. Stream treatment consisted of the introduction of insecticide at a concentration of 1 part insecticide in 10,000,000 parts of water over a 15-minute period. For the airsprays the 'low dosage' technique was used. A spray aircraft emitting 1 gal of 2 lb/gal mixture/flight mile laid down a swath across a stream. In addition to interest in efficacy as blackfly larvicides, the study involved an examination for any selective effects on non-target invertebrates. Cidial, Gardona and Fenitrothion were not satisfactorily effective. Methoxychlor, Abate and Dursban all gave satisfactory control (*elimination of most* blackfly larvae for a distance of at least ¾ mi below the line of application). There was little evidence of any consistent selective effects on non-target organisms.

Since 1969 Methoxychlor has been recommended for aerial larviciding. Starting in 1971 Abate was recommended for stream treatment, to comply with wishes of the (then) federal Department of Fisheries.

a. *Particulate Formulations*

I am endebted to Dr. H. Hurtig for calling to my attention an article in Nature (Kershaw *et al.* 1965) describing some U.K. studies on the use of a particulate formulation as a blackfly larvicide. The rationale was that insecticide in a particulate form, of a size range of the particles ingested by blackfly larvae, might be taken up selectively by filter feeders. The U.K. studies reported that within certain dosage limits only blackfly larvae were affected.

Through the cooperation of the Shell Research Centre, Sittingbourne, we obtained some of the particulate formulation of DDT. Our tests showed that while this material affected mainly blackfly larvae, some other filter-feeders, such as certain caddisflies, were also killed.

Through the courtesy of the Johns-Manville Co. in Manville, New Jersey, and Cyanamid of Canada Ltd., particulate formulations of Methoxychlor and Abate respectively were obtained. Whereas the DDT particles were mostly in the 8-15 μ size range, the Methoxychlor and Abate particles had a greater size range, but with a predominance of particles in the 15-25 μ range.

These materials have a highly selective action, and for practical purposes affect only Philopotamid caddisflies in addition to blackfly larvae Limited airspray tests were also encouraging. Much remains to be done by way of studies on the most effective particle size range, and specific gravity of the formulation, for example. However, it is safe to predict that within several years particulate formulations will be the larvicides of choice.

2. Adulticiding

Whereas finding effective and safer compounds to replace DDT for larviciding did not prove difficult, a DDT-replacement for adulticiding posed more of a problem.

Candidate compounds (oil formulations) were assessed by use of a London-Model 25 thermal-aerosol generator and caged blackflies exposed 350 yd downwind of a fogging line. Eleven compounds or mixtures were tested; several of these were tried at various emission rates, although the DDT standard of 0.28 lb/100 yd front was used as a basis of comparison (Methoxychlor, Malathion, Malathion-Lethane, Malathion-Methoxychlor, Malathion-Dibrom, Dibrom, Korlan, Dowco-214, Baygon, Baygon-Baytex, and Fenitrothion).

Only Baygon, Dibrom, and Korlan proved effective. Dibrom was ruled out because of fogging machine gumming problems sometimes encountered even when a recommended additive was incorporated in the spray mix. Korlan is a reasonably promising material, but Baygon is in a class by itself, giving rapid knockdown and 90-100% mortality in all tests under a variety of conditions. In addition, in comparison with the standard DDT emission rate of 0.28 lb/100 yd front. Baygon (a carbamate) is effective at an emission rate of 0.035 lb/100 yd front.

A wettable powder formulation was also tested and was equally effective; however, further tests would be necessary to determine if any deposits build up in the feed lines of the fogging machine.

A somewhat abortive attempt to test the Baygon wettable powder, suspended in oil, as an air-spray adulticide did show considerable promise, and is considered to be worth further study. Fuel oil is available at all locations where control operations are carried on. Significant savings would accrue if insecticide shipments involved only a powder rather than including a diluting or suspending agent.

B. Mosquitoes

1. Larviciding

Although no experimental airspray operations have been conducted against mosquito larvae, both Dursban and Abate have given excellent control of *Aedes* larvae in a practical operation involving an area of 25 sq. mi. The dosage of Dursban was 0.05 lb/a; that of Abate 0.015 lb/a. In contrast, Methoxychlor must be applied at a dosage of 0.2 lb/a to obtain effective control.

2. Adulticiding

Casual observations during an area test of Baygon fogged primarily for blackfly control suggested that this material may be equally effective against adult mosquitoes.

Baygon 70% wettable powder, suspended in water, was tried as a "back-yard" spray. The grass and surrounding vegetation of a 6000 sq. ft. area was wetted with 6 gal of wettable powder mix (½ oz a.i./US gal). Although because of weather conditions during several series of tests results were not conclusive, they were sufficiently promising to warrant further study.

A material marketed in the U.S. under the name of Mosquito Beater (vermiculite granules impregnated with a mixture of naphthalenes), and for which claims are made as a mosquito repellent, did not prove effective under Canadian conditions.

Future Needs

It is evident that although few if any materials have the superlative characteristics of DDT for biting fly control there are effective replacement compounds. Future research emphasis should be placed on formulations and methods of application. The significance of particulate formulations of blackfly larvicides has been emphasized.

There is a need to try ULV air-sprays under Canadian conditions. Unfortunately the intended Armed Forces development of a ULV capability was scrubbed. There is now on the market in Canada a ULV (LECO) fogging machine. Assessment of this equipment should be carried out.

In these times when the justification of pollution of any kind is being questioned, it is suggested that stricter supervision of chemical control of biting flies is in order. It would seem reasonable to suggest that levels of biting fly activity below which chemical control would not be permitted should be established.

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INSECTICIDES USED FOR THE CONTROL OF BITING FLIES AND THEIR POLLUTION POTENTIAL

Jadu G. Saha
Canada Agriculture Research Station
University Campus
Saskatoon, Saskatchewan

INTRODUCTION

The usefulness of chemicals in controlling insect pests of crops and forests, as well as the insect vectors of human and animal disease, has been recognized from the beginning of this century. The use of pesticides had a modest beginning – with only a few inorganic compounds of arsenic and copper and a few naturally occurring organic insecticides such as Pyrethrum and rotenone. But pesticides really came of age with the discovery of DDT and 2,4-D during World War II. Since then hundreds of synthetic organic chemicals have been discovered and used by man to improve the quality and quantity of food and fibre produced and to improve man's health and welfare. The use of pesticides in agriculture has revolutionized farm practices and dramatically increased crop yields. The effectiveness of the modern pesticides against a wide range of disease vectors has made possible the control of many important diseases which previously defied all efforts at control. Epidemics of classical plague and murine typhus no longer threaten mankind. Malaria has been eradicated from large areas of the world and is under dramatic control elsewhere.

In bringing about this revolution in human health and welfare, the increasing use of pesticides has also resulted in new problems. The very stability and persistence that has made DDT the ideal weapon for malaria eradication has caused widespread distribution throughout the environment and has adversely affected some species of wildlife and fish. Resistant races of pests have also appeared in response to intensive use of pesticides. This has led to the discovery and use of new classes of insecticides whose effects on the environment are even less understood than those of DDT.

Numerous modern technological developments threaten the quality of our environment. Although pesticides are a small part of this productive technology, they have had more than their due share of blame. Insecticides, particularly those used for the control of biting flies, constitute only a small portion of total pesticides used (including other insecticides, herbicides, fungicides, nematocides, etc.) by man today. This review will attempt to summarize our present-day knowledge of the pesticides used for the control of biting flies and evaluate their potentials as pollutants of the environment.

Insecticides Commonly Used for Biting Fly Control

Numerous insecticides have been tested and used for the control of insects commonly referred to as biting flies. While some species of these insects are vectors of human and animal diseases, others are only nuisance insects. This review will not attempt to discuss all the insecticides that have been or are being used to control all the different species of biting flies. Rather it will be limited to the insecticides that are used frequently to control the more important species of biting flies.

Mosquito

DDT is still the principal chemical used in the campaign against malaria, which now employs about 100 million pounds of technical DDT per annum (Brown 1970). The stated objective in the campaign is not to eradicate the *Anopheles* mosquito vectors but to terminate the transmission of the malaria infection by them. Virtually all DDT applications are made inside houses, the residual adulticide being applied to the inner walls and usually the ceilings at a rate of 200 mg of DDT per sq. ft. Small amounts of dieldrin and lindane have also been used for this purpose.

DDT is also used as a larvicide by adding it to water bodies for the control of culicine mosquitoes, mainly of the genera *Aedes* and *Culex*. Sometimes larvicidal control is supplemented by aerosol fogs of DDT as adulticides. In North America several species of mosquitoes have been incriminated in the transmission of a variety of arbovirus diseases of man and horses (at least four in Canada). The great majority of mosquitoes can be classified as pest species which interfere with recreation and work out-of-doors and thereby affect public welfare and depress real estate values. The use of DDT for the control of these mosquitoes has recently been severely restricted or discontinued in the U.S.A., Canada and many other developed countries. In these countries DDT has been replaced by a number of organophosphorous (OP) insecticides including Baytex (fenthion), Dursban, Abate, and parathion, and carbamate insecticides such as Sevin and Furadan. In the California Mosquito Control Programs OP compounds are widely used as larvicides. The average number of treatments per year is four, but in some areas up to ten may be necessary (Mulla *et al.* 1966; Mulla 1966a). Parathion has been used widely for this purpose at the rate of 1 lb/acre. In Asia, the use of DDT to control *Culex fatigans*, the vector of filariasis, has been discontinued due to the development of resistance. The OP compounds, fenthion, Dursban, and malathion, are likely to replace DDT for this purpose (Brown 1970). For larvicidal applications against *Aedes aegypti*, the vector of haemorrhagic dengue in Asia and of yellow fever in Africa, the use of DDT has been discontinued in most areas due to resistance and is being replaced by malathion and Abate.

The toxicities of some selected insecticides to larvae of *Anopheles albimanus* (Metcalf *et al.* 1969) are given in Table 1.

TABLE 1

Toxicities of selected insecticides to larvae of *Anopheles albimanus* (Metcalf *et al.* 1969)

Insecticide	Larval LC_{50} in ppm
Dursban	0.006
Abate	0.011
DDT	0.015
Fenthion (Baytex)	0.016
Malathion	0.100
Arprocarb (Baygon)	0.230

Blackfly

In many parts of the temperate and subarctic regions, i.e. in Canada and the U.S.S.R., dense populations of blackflies constitute a serious menace to man and to domestic animals. They are, if nothing else, a serious menace to the enjoyment of outdoor life, especially in the forested areas of Canada. They attack quietly and the victim may itch for weeks. A severe attack can result in a bout of "blackfly fever" which includes fever, headache, nausea and swollen, painful neck glands.

In certain areas adjacent to large rivers in Saskatchewan, Alberta and British Columbia, periodic outbreaks of *Simulium arcticum* and related species are so massive as to drive animals out of the pastures and even cause the death of animals not sheltered immediately (Fredeen 1972). In central Saskatchewan more than 1,300 animals were killed by *S. arcticum* between 1944 and 1948. Apart from deaths from the poison injected into the animal body there may be indirect losses to the livestock producers from reductions in milk production and animal weights, as well as interruptions in the breeding season.

The species affecting poultry are *S. meridionale*, *S. rugglesi* and some species of *Eusimulium*. They are vectors of Leucocytozoon blood parasites of birds. These parasites cause a form of malaria that has occasionally caused massive losses among flocks of turkeys, ducks, geese and chickens located near small rivers (Fredeen 1972). Man and animals are never affected.

In contrast to the situation in Canada and the U.S.S.R., the interest in *Simulium* in many parts of tropical Africa as well as more limited areas in Central America -- particularly Mexico and Guatemala – is not so much as a biting pest but in its role as vector of human onchocerciasis (Brown 1970). The popular term for this disease in Africa is "river blindness".

Blackfly larvae and pupae live only in running water and each species is very specific as to the kind of river or stream it inhabits. In the case of onchocerciasis in Mexico and Guatemala, the main species prefer to breed in comparatively small streams, sometimes mere trickles heavily covered with undergrowth. In contrast, *S. damnosum*, the main vector of African onchocerciasis, breeds in some of the largest rivers in that continent such as the Niger, the Congo, the Sudan and Victoria Nile (Muirhead-Thomson 1971). In Canada the breeding sites for *S. arcticum* are in rapids of large mountain-fed rivers such as the Saskatchewan, the Athabaska and a few rivers in British Columbia, while the breeding sites of the species affecting poultry are in small rivers (Fredeen 1972).

Direct attack against the aquatic stages of *Simulium* in these rivers still remains the only effective method for their control and DDT was the larvicide of choice for this purpose. It was used for more than 20 years for the control of blackflies in the Saskatchewan River and it is still being used in Africa for the control of *S. damnosum* (W.H.O. 1966). In Canada the use of DDT for the control of blackflies has been discontinued due to the possible harmful effects on the aquatic environment and methoxychlor is considered to be a promising replacement insecticide for this purpose (Fredeen 1972). Dursban and Abate are also under investigation for the control of blackflies in Africa as well as Canada. An ingenious approach is being made in Africa to use DDT as *Simulium* larvicide (Kershaw *et al.* 1968). Since these larvae are particulate feeders, DDT is being formulated in such a way that it is readily ingested by *Simulium* larvae, but less readily available to other stream invertebrates and fauna.

Midges and Gnats

In many areas of North America biting midges of the genus *Culicoides* are of more serious concern than mosquitoes, since these insects can easily enter dwellings through 16-mesh screens which exclude mosquitoes. These insects also greatly reduce property values, particularly along the eastern coast where they are abundant. The bites of most species are accompanied by immediate intense sharp pain and irritation, followed by the development of red wheels so that the victim may look as if he is suffering from measles. Some victims scratch themselves severely resulting in secondary infections. In parts of Central and South America and the West Indies, several species of *Culicoides* have been incriminated as the intermediate hosts of filarial worms. Viruses of Eastern and Venezuelan encephalitis have also been isolated from *Culicoides*. Species of *Culicoides* which prefer to feed on birds were also shown to be vectors of *Haemoproteus* occurring in domestic ducks, spruce grouse, and many other birds in Algonquin Park, Ontario (Fallis and Bennett 1961).

Culicoides larvae may be found in mud, sand, and debris at the edges of ponds, springs, lakes, creeks, ditch margins or margins of small bodies of still or slowly running water; compost piles, rotting leaf mold, in peaty soils, manure, and any other vegetable matter that stays wet constantly.

Several organochlorine insecticides such as DDT, dieldrin, chlordane, aldrin, BHC, and toxaphene have been used for the control of *Culicoides* larvae (Weinburgh and Pratt 1962). Ground and aerial sprays of DDT have also been used for control of adult *Culicoides*. The wisdom of using these persistent insecticides is questionable today. Temporary relief, at least inside homes, can be obtained by treatment of window screens with Pyrethrum in oil or malathion in ethanol solution.

The control of non-biting midges and gnats is a matter of serious concern in many countries ranging from temperate to tropical. At certain seasons of the year swarms of these insects, which are attracted by light, may invade streets and houses in vast numbers, generally making living conditions extremely uncomfortable or even intolerable on occasions. One of the best known representatives of this group is the Clear Lake gnat which has been thoroughly studied not only from the direct pest control point of view but also because of pioneer work on the accumulation of TDE or DDD in fresh-water habitats (Lindquist and Roth 1950; Lindquist *et al.* 1951; Hunt and Bischoff 1960; Cook and Conners 1963). As serious ecological problems arising from the use of TDE became apparent, its use was replaced with that of methyl-parathion. This compound when used at 3 ppb concentration proved highly toxic to early instar larvae and there was no problem of persistence or accumulation within the habitat (Hazeltine 1963; Cook and Conners 1963).

In Florida, BHC and EPN were extensively used in midge control in the early 1950s, but were only partly successful. Baytex (fenthion), however, has proved more successful in recent operations (Patterson and von Windeguth 1964a and b). A variety of other organophosphorous compounds such as malathion, Dipterex and DDVP have also been found to have possibilities for use as larvicides with very little harm to fish (Hilsenhoff 1959). The ever-threatening possibility of resistance developing on the part of the pest has led to the continued search for more effective compounds (Mulla and Khasawinah 1969; Anderson *et al.* 1965), although there appears to be no easy solution to the problem (Muirhead-Thomson 1971).

Properties of Insecticides Used for Biting Fly Control

Mention has been made of the major insecticides that have been or are being used for the control of only a few important species of biting flies. The names of the insects mentioned above do not include all the species of biting flies, as there are many other species that are significant pests.

Physical Property

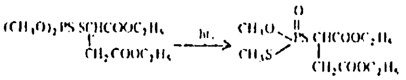
DDT, DDD (TDE), and methoxychlor are the only important organochlorine compounds that are now used for the control of biting flies (Table 2). A number of organophosphorous compounds, including Baytex, malathion, parathion, methylparathion, Abate, diazinon, dichlorvos (DDVP), Dursban, and dibrom (Naled), are also used for this purpose. In contrast only two carbamate insecticides, Sevin and Furadan, have found some limited use. DDT has the lowest vapour pressure of the insecticides listed in Table 2 and dichlorvos the highest. Thus DDT would be expected to be least volatile and dichlorvos would be most volatile. It should be remembered that vapour pressures are determined in a closed system under thermodynamic equilibrium conditions. But insecticides are always used under kinetic conditions and vapour pressure data do not reflect their true volatility. Under field conditions any given insecticide volatilizes many times faster than that indicated by its vapour pressure. It has been shown that 40% of DDT applied to leaf surface would volatilize into the atmosphere in 48 hr at 33°C and with only 2 mph wind (Que Hee *et al.* 1972). Thus if the insecticide is stable, most of the applied toxicant will volatilize from the target into the atmosphere within a matter of days or weeks unless it is incorporated into the soil or it is present in solution in water.

Most of the insecticides used for biting fly control are applied to water bodies as larvicides. The notable exception is the use of DDT for mosquito control in malaria eradication programs where it is mostly applied inside houses. Generally speaking the insecticides used for biting fly control are not particularly soluble in water (Table 2). Their solubilities in water are from a few parts per billion to about 145 ppm (malathion). Only dichlorvos has appreciable solubility in water. The latent heat of solution of many of these insecticides is in the order of 13 kcal per mole, which means that they would be strongly bound to colloidal surfaces such as organic and inorganic suspended particulate matter in the aquatic environment. Therefore the equilibrium concentration in water would be extremely low, at least lower than that indicated by the solubility data.

Stability

The stabilities of the compounds listed in Table 2 vary widely. In general the three organochlorine compounds are more stable than the organophosphorous or the carbamate insecticides. The p,p'-isomer of DDT is thermally stable, decomposition taking place only above 195°C. DDT undergoes dehydrochlorination to DDE in the presence of alkali. Methoxychlor is similar to DDT in its chemical properties, but its dehydrochlorination takes place considerably more slowly. Thus, while the rate constant of the reaction of DDT with KOH in alcohol at 40.19°C is 0.186, that of the p,p'-isomer of methoxychlor at the same temperature is 0.00097 (Melnikov 1971).

Malathion on prolonged heating at 150°C is converted to the corresponding thioloisomer:



Malathion is readily decomposed by acid or alkali but the reaction follows different paths in the two media:

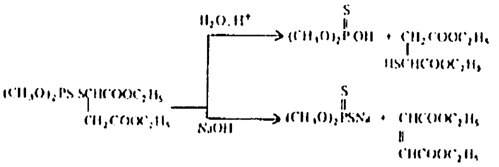


TABLE 2

Vapour pressure and water solubility data of selected insecticides used for biting fly control

Name	Vapour press. mm Hg	Solubility in water ppm
DDT	1.9×10^{-7} at 20°C	0.037 at 20°C
DDD (TDE)	–	insol.
Methoxychlor	–	0.1 at 25°C
Malathion	4×10^{-5} at 30°C	145
Parathion	3.78×10^{-5} at 20°C	24
Methylparathion	0.97×10^{-5} at 20°C	25
Abate	–	insol.

TABLE 2 (Continued)

Diazinon	8.4×10^{-5} at 20°C	40
Dichlorvos (DDVP)	1.2×10^{-2} at 20°C	10,000
Dursban	1.87×10^{-5}	2 at 25°C
Baytex	3×10^{-5} at 20°C	54 at 20°C
Naled (Dibrom)	–	insol.
Sevin (Carbaryl)	5×10^{-3} at 26°C	40

It is also readily converted to the oxygen analog in the presence of oxidizing agents or in biological systems (Melnikov 1971).

Parathion is gradually converted to the thiolo isomer even at a lower temperature (100°C) than malathion. It is rather stable in acid. At ph 1–5 about 50% is hydrolyzed in 690 days at 20°C, and in 17 to 20 hr at 70°C. But it is readily hydrolyzed in alkaline medium. The rate of hydrolysis of methylparathion is considerably higher than of parathion, especially in alkaline medium. Diazinon is not as resistant to hydrolysis as parathion. In acid medium it is hydrolyzed 12 times as rapidly as parathion, and in alkaline medium the hydrolysis goes on at practically the same rate. Dursban is also slowly hydrolyzed in acid or alkaline medium. But fenthion (Baytex) is more resistant to hydrolysis and heating than methylparathion. In aqueous solution no hydrolysis of Abate takes place at pH 8 at room temperature even after several weeks. The half-life of dichlorvos in pure water at 20°C is 61.5 days. But the pure compound in the presence of traces of moisture decomposes readily with the formation of acidic products that catalyze further decomposition of the compound. To stabilize the technical grade product 2–4% epichlorohydrin is added, which ties up the acidic substances and improves the conditions for storage of the compound. With respect to hydrolysis, naled is more stable than dichlorvos. Sevin is resistant to the action of water, light, and the oxygen of the air at room temperature. But is is rapidly hydrolyzed in alkaline medium. Furadan is also unstable in the presence of alkali.

The photodecomposition of all the compounds listed in Table 2 has not been studied. It is expected that they would be decomposed by light, although the rates may vary widely.

Metabolism

Information on the degradation of insecticides in the biological system is essential for the rational assessment of hazards arising from the use of these compounds for pest control. Identification of the metabolites and evaluation of their toxicological properties are essential for proper assessment of hazards of terminal residues in plants and animals. Metabolism studies are also very important for the elucidation of the intoxication and detoxication processes that occur in animals, plants, and microorganisms.

Probably no single insecticide has been more widely investigated for metabolism than DDT. Its metabolism has been investigated in several species of animals including man, insects, birds, and fish (Table 3). The degradation of DDT by soil and soil microorganisms is also well known. In insects DDT is converted mainly to DDE while in mammals DDA and DDE are the major metabolites. Recently, there has been increased evidence for the conversion of DDT to DDD by various microorganisms, insects, mammals, and also by birds. Although DDE is less toxic to mammals than DDT it is the major cause of the production of thin-shelled eggs by raptorial and fish-eating birds. Thus metabolism of a toxic substance to a product having less acute toxicity to mammals does not necessarily mean that the metabolite would be less harmful in the environment. The chronic toxicity of the compound or its metabolites is far more important in assessing environmental hazard.

Although methoxychlor has been known for more than 20 years very little is known about its metabolism, although it is known to be excreted by animals at a rate much faster than that of DDT (Kapoor *et al.* 1970).

In contrast to DDT most of the organophosphorous and carbamate insecticides are rapidly metabolized. Oxidative and hydrolytic pathways are important for the detoxification of these insecticides by various organisms. The metabolites are usually far less toxic than the parent compound and are not stored in the animal body to any great extent. The

TABLE 3

Availability of information on the metabolism of insecticides used for blackfly control (Menzie 1969; Fukuto and Sims 1971)

	Information available for metabolism by				
Insecticide	Mammals	Insects	Birds	Fish	Soil/bacteria
DDT	+	+	+	+	+
DDD	+	+	+	–	–
Methoxychlor	+	+	–	–	–
Malathion	+	+	+	–	+
Parathion	+	+	–	+	+
Methylparathion	+	+	–	–	–
Abate	+	–	–	–	+
Diazinon	+	+	–	+	+
DDVP	+	+	–	+	+
Dursban	+	–	–	+	–
Baytex	+	+	–	–	–
Naled	+	–	–	–	–
Sevin	+	+	–	–	–
Furadan	+	+	–	–	–

metabolic fate of the organophosphorous and carbamate insecticides used for blackfly control has been studied in mammals and insects. But metabolism of these insecticides in birds has not been studied. Exception is the case of malathion. Although there is no *a priori* justification in assuming that the degradation of these insecticides by birds will be different from that by mammals, the possibility cannot be ignored. Metabolism of these compounds by fish also has not been studied with every insecticide (Table 3). Since these insecticides are largely used as larvicides in the aquatic environment, their metabolism by fish and fish-eating birds should be studied.

Effects On Non-Target Organisms

In most freshwater habitats where insecticides are applied to control a particular undesirable organism such as mosquito or blackfly larvae, the idea of what constitutes a non-target organism is usually understood to mean simply those organisms whose destruction is not intended. In practice, the distinction tends to be less general and to refer specifically to organisms which play a key role in the ecology of the habitat, particularly with regard to species which form vital links in the food chain. However, the distinction is not rigid as there may be cases where "non-target" organisms may become the target species.

In many rivers and streams the larvae of caddis flies (Trichoptera) and the nymphs or naiads of mayflies (Ephemeroptera) are considered to form important food sources for trout and other valuable fresh-water fish. In some areas these insects are produced in such enormous numbers as to constitute a nuisance or pest, and their immature stages are then liable to be the direct target of planned control operations with insecticides (Lieux and Mulrennan 1955; Fredeen 1972). The same flexibility of term applies to "undesirable" fish. Carp rank high on the list of undesirable fish in this country but it is a major source of food in many other countries.

These rather unusual exceptions should not obscure the fact that in any particular water the distinction between target and non-target organisms remains clear, and that the ideal of control operations should be to control the population of the particular undesirable species at pesticide concentrations which will have the minimal adverse effect on the rest of the fresh-water biota.

The use of insecticides for the control of biting fly larvae is perhaps the best example of the application of toxic chemicals to fresh water. The following discussion is related to the effects of this use on non-target organisms such as fish and aquatic invertebrates.

Fish

One of the first critical studies into the possible hazards of DDT to fish and fresh-water organisms originated in the widespread application of this compound by aircraft for control of forest insects in the U.S.A. and in Canada (Hoffman and Droor 1953). In the forest areas of Montana and Yellowstone National Park, for example, there was heavy DDT spraying against spruce budworm from 1952 to 1956 over an area of more than 2 million acres. A few months after spraying there were reports of dead and dying fish in the Yellowstone River within and below the sprayed area. Densities of dead fish (mostly whitefish and brown trout) of the order of 600 fish in less than 300 yd of stream were noted.

In Canada, extensive forest areas in New Brunswick and Quebec were sprayed with DDT from aircraft for spruce budworm control between 1952 and 1958. These applications were responsible for reducing the salmon population in the treated area (Kerswill and Elson 1955; Elson 1967; Webb 1960). In the very early phases of DDT aerial spraying, the application rate was 1 lb/acre which was subsequently reduced to 0.5 lb/acre and finally to 0.25 lb/acre in New Brunswick. Although these are not examples of the use of DDT for biting fly control, these studies do indicate the possible harmful effect of the introduction of DDT into fresh water.

Apart from direct toxic effect of DDT to fish, there may be indirect effect on fish populations due to destruction of food supply. Fish may then migrate from the contaminated water or may die of starvation. This was observed at Jinja in Uganda in 1956 when DDT was used to control *Simulium* larvae in the Victoria Nile. The DDT treatment eliminated not only *Simulium* larvae but probably all lithophilous insect fauna which was the main diet of several species of fish. One of these – *Mastacembelus* – was a specialized feeder on these insects and they either died of starvation or were compelled to move away (Corbet 1958). In contrast, another species of unspecialized feeder such as *Clariallabes*, which had previously fed on 90% lithophilous insects, was able to survive by feeding on plants, molluscs, etc., unaffected by the DDT treatment.

In addition to this type of indirect effect of DDT on fish, there is some evidence of immediate or direct effect on fish following DDT-treatment of rivers for *Simulium* control. For example, the application of DDT emulsion at the rate of 0.1 ppm for 30 min. to the River Niger at Kouroussa in Guinea led to high fish mortality within 20 min. of application and up to 10 km below the application point (Muirhead-Thomson 1971). Laboratory tests on several species of tropical fish later showed that irreversible damage could be produced after some hours' exposure to concentrations of DDT as low as 0.01 to 0.05 ppm. In contrast, the organophosphorous compound Baytex could be tolerated by these fish at concentrations up to 3 ppm for many hours (Post and Garms 1966). Another example of such immediate effect of DDT on fish was observed in Sudan in 1957. DDT was applied by aircraft at a calculated concentration of 0.11 ppm over about 110 min. of flow to the Blue Nile at Khartoum to control chironomid midges (Brown *et al.* 1961). Numbers of fish were killed, and examination of dead specimens showed DDT concentrations up to 79 ppm.

In contrast to these experiences with DDT in African waters it is significant to note that in one of the early classic examples of *Simulium* control in large rivers, namely DDT treatment of the Saskatchewan River in Canada (Arnason *et al.* 1949), no adverse effect on fish life could be detected following aerial treatment at 0.1 ppm DDT for 30 min. DDT was used sparingly for *Simulium* control in the Saskatchewan River for more than 20 years and at the end of this period negligible DDT residues were found in several species of fish from this river (Fredeen *et al.* 1971).

Of particular concern in many mosquito control campaigns has been the non-target species *Gambusia affinis* (mosquito fish) which feeds on mosquito larvae and plays an important role in their biological control. In the California Mosquito Abatement Programs, OP compounds – including parathion – have been widely used. The average number of treatments per season is four, but in some areas up to 10 treatments are necessary. In such circumstances fish like *Gambusia* as well as other fresh-water fauna – are under very heavy insecticide pressure and search should continue for non-insecticidal control methods.

Aquatic Invertebrates

Although it has been recognized for many years that application of DDT to rivers was liable to have drastic effect on the ecological balance, systematic investigations on the problem have been few and far between. Most of the studies were limited to the effect of DDT treatment on fish. Reference was made earlier to the side effects of *Simulium* control operations on the Victoria Nile at Jinja, Uganda, where application of DDT completely eliminated the lithophilous insect fauna.

A systematic attempt to study the ecological effects of DDT treatment of streams was made in the River Manafwa in Uganda in 1960, at a point where the stream was about 12 ft wide flowing over stones and boulders (Hynes and Williams 1962). DDT was applied at the rate of 0.1 ppm for 30 min. The most drastic effect appeared to be in three insect predators, *Neoperla, Hydropsyche*, and *Cheumatopsyche*, which were reduced both in number and size. This in turn has led to an increase in numbers of prey organisms such as mayfly nymphs and *Simulium* larvae below dosage point. Many Ephemeroptera were noticeably smaller below dosage point than above, indicating that the exposed generation had been killed and had become re-established from eggs. In the U.S.A. it was found that a somewhat similar dose of DDT – 0.1 ppm for 20 min. – appeared to have very little effect on riffle inhabiting arthropods other than blackfly larvae (Jamnback and Eabry 1962).

From the few examples cited above, as well as many other scattered observations which have not been stated here, it is rather difficult to get anything other than a confused picture about the impact of DDT on stream invertebrates. Much of this may be due to the wide range of conditions in rivers and streams. In addition, in some of the studies the observation period was limited to a few days following application of DDT while in others the observation periods were months or years. These longer term observations have shown that some genera of stream invertebrates which appeared to be almost entirely eliminated within a few days of treatment make a very rapid recovery to normal populations within a few weeks or months, while others appear to be more permanently affected.

The use of DDT and other organochlorine insecticides for the control of biting flies has been almost completely superseded by the organophosphorous insecticides, and to a much lesser extent by the carbamates. These changes have come in a period when the scientists and the public have become aware of the need to assess the impact of such chemical treatments on the ecology of the aquatic environment. Many of the new insecticides are lethal to the target organisms at very low concentrations. It may be expected that they may be equally fatal to non-target organisms as well. To offset this apprehension is the increasing weight of evidence, based on extensive chemical analyses of water, mud, aquatic flora and fauna of treated water bodies, about the general non-persistence of these compounds in the environment, and the fact that they are easily biodegradable and they may disappear completely in a matter of days after application.

One of the first organophosphorous compounds to be thoroughly investigated from the point of view of general ecological impact on fresh water was methyl-parathion which was used from 1962 onwards as a replacement for TDE (DDD) for the control of Clear Lake gnat (Cook and Conners 1963). Although this compound is known to have a much higher mammalian toxicity than any other used as an aquatic pesticide, the very low dosage (3 ppb) used was adequate for the control of early instar *Chaoborus* larvae, but had very little effect on non-target organisms.

Baytex (fenthion) has also been widely used for controlling mosquito and non-biting midge larvae. Applications of a granular formulation of Baytex to small ponds showed that at a concentration of 0.025 ppm it was lethal to Chironomid larvae but was non-toxic to such aquatic organisms as Copepods, Ostracods, Hydra, Annelid worms, snails and clams (Patterson and von Windeguth 1964a). The usual dosage of Baytex may be lethal to shrimp and Amphipods found in shallow areas of lakes. However, shrimps would survive in deep waters and the total effect on shrimp populations may not be significant. Among other invertebrates it appears that nymphs of dragonflies are more affected by Baytex used in mosquito control operations than most other non-target species (Whitsel *et al.* 1963).

In the case of Dursban – one of the most powerful of the new organophosphorous larvicides – it has been clearly shown that at a certain critical range comparatively small increases in concentration may determine how lethal the impact of this chemical is on fresh-water fauna. *Culex tarsalis* larvae can be controlled with an application of 0.005 lb of Dursban/acre without any noticeable ill-effect on non-target organisms. But the highly sensitive mayfly nymphs are affected at a dosage level of 0.01 lb/acre (Mulla *et al.* 1966). Aerial application of Dursban at 0.01 to 0.02 lb/acre resulted in noticeable die-off of practically all arthropods (Moore and Breeland 1967). Thus one must be extremely careful in the application of Dursban for mosquito control and aerial application of Dursban should be avoided, as it may result in uneven distribution leading to high concentrations in localized areas.

There are conflicting reports in the literature on the effects of Abate, another highly successful organophosphorous larvicide, on non-target organisms. In one report, field application of 0.25 lb/acre had no noticeable mortality on Odonata, *Chaoborus* larvae, Copepods, Ostracods or fairy shrimps (von Windeguth and Patterson 1966). In contrast to this observation, treatment of a lake at the rate of 0.039 lb/acre proved toxic to nearly all insects in the lake (Fales *et al.* 1968). The impact of Abate was carefully examined in connection with mosquito control of temporary pools along the shore line of Lake Michigan in Wisconsin (Porter and Gojmerac 1969).

Although the application of Abate at 0.03 lb/acre was effective against mosquito larvae, this treatment also eliminated larvae of the caddis fly and seriously affected early instar Libellulid naiads (Odonata). The Abate treatment also eradicated *Cladocera* but had no effect on Amphipods, Isopods, Ostracods and Copepods.

Effect on Environment

The only generalization that can be made about the properties of insecticides used for biting fly control is that there is great variation. The impact of a given insecticide on the environment is largely determined by its toxicity and persistence. The two properties are especially important ecologically and the range of effect varies widely for both. The insecticide may kill non-target organisms, have sub-lethal effects or no effect on them at all. Some may persist in the environment for years while others may disappear in a matter of days or weeks.

The most obvious effect of a pesticide is death. It is easily perceived in vertebrate species and its ecological effects can be assessed more easily than others. Animals may take up the pesticide through their body surface, through respiratory organs or the alimentary canal. Terrestrial vertebrates mainly obtain pesticides orally and for warm-blooded vertebrates the common test is the determination of acute oral LD_{50}.

Some of the insecticides, such as Furadan, parathion, and methylparathion, used for blackfly control, are extremely toxic (6-50 mg/kg) to vertebrates (Table 4). They are hazardous to the operators, especially when no proper precaution is taken. They also should not be used in areas where human exposure is likely immediately following their application. Several deaths were reported from India when parathion was used for mosquito control inside houses. Enough toxic residues remained for hours in the house sprayed with parathion to cause death of the people sleeping there. This is one reason why extremely toxic chemicals cannot be used as mosquito adulticides, especially in countries where the majority of the people cannot read the label. DDT, Abate, diazinon, DDVP, naled, Dursban, Baytex and Sevin can be considered very toxic (50 to 500 mg/kg) to mammals, while DDD, methoxychlor and malathion are moderately toxic (500 mg to 5 g). However, it is unlikely that the proper use of any of these compounds would be hazardous to man himself, so far as acute toxicity is concerned.

TABLE 4

Vertebrate toxicity of some insecticides used for blackfly control

	Toxicity	
	Rat	Bird
Insecticide	(acute oral LD_{50} mg/kg)	(acute oral LD_{50} mg/kg)
DDT	113	> 1300 (chicken)
DDD (TDE)	3400	–
Methoxychlor	6000	–
Malathion	2800	> 850
Parathion	6-12	–
Methylparathion	25-50	–
Abate	151	80-100 mallards 18-55 pheasants
Diazinon	76-320	40.8 chicken 14.7 goose
DDVP (dichlorvos)	80	7.8 mallards
Naled (dibrom)	430	46 ducks
Dursban	150	70-80 mallards 8-18 pheasants
Baytex (Fenthion)	215-245	15 ducks
Sevin	500	> 1500 sharptail
Furadan	–	38.9 chicken

While it is possible to compare the acute oral toxicities of these compounds from the LD_{50} values to rats, it is almost impossible to compare their toxicities to birds. Acute oral LD_{50} data are not available for these insecticides for any one species of bird. However, it is unlikely that direct application of these compounds on any wild bird would prove fatal, especially at the dosage used for biting fly control.

In fish the intake of pesticides is mainly through their gills and to some extent through their food. The acute toxicity of pesticides to fish is usually expressed by TL_m values, i.e. the concentration sufficient to produce 50% mortality within a specific period of time. Many of the insecticides used for biting fly control have high acute toxicity to fish (Table 5). But the concentrations required for effective control of larvae of these insects are usually very low and thus in most cases present no immediate hazard to fish. It has been pointed out before that with some of these insecticides survival or death of fish may depend on a rather small change in concentration of the insecticide in water.

Sublethal effects of pesticides are more difficult to measure than acute toxic effects and laboratory experiments on chronic toxicity may not detect the long-term effect. In the easy conditions of laboratory life the consequences of sublethal poisoning are not likely to be serious, but in the natural habitat of the animal, a very slight loss in efficiency or an alteration in behaviour may have serious consequences. From an ecological point of view sublethal effects are of great significance. They are extremely difficult to measure and assess, and there is little evidence to show how important, in fact, they are in the field.

A very wide range of sublethal effects has been attributed to pesticides but few have received systematic study. Most of the work is on the effects of insecticides on the reproduction of galliform birds. Effects on the number of eggs laid, hatching and

TABLE 5

Toxicity to fish of insecticides used for biting fly control

Insecticide	Fish	Conc. of toxicant sufficient to kill 50% of test animals within the specified period TL_m (ppm)
Low to moderately toxic		
Carbaryl	Rainbow trout	1.35^{96h}
		3.5^{24h}
Abate	Rainbow trout	1.0^{96h}
		1.9^{24h}
	Bluegills	54^{24h}
	Guppies	200^{24h}
Methylparathion	–	–
DDVP	Rainbow trout	0.5^{24h}
Fenthion	Rainbow trout	0.76^{96h}
	Bluegills	0.67^{96h}
	Guppies	3.32^{24h}
Parathion	Goldfish	1.5
Naled	Rainbow trout	0.07^{24h}
Dursban	Guppies	0.22^{24h}
Diazinon	Rainbow trout	0.38^{24h}, 0.09^{96h}
DDT	Bluegills	0.0099^{24h}
	Goldfish	0.1
TDE	Goldfish	0.90
Methoxychlor	Goldfish	0.06
Furadan	Rainbow trout	0.28

viability of the progeny of birds dosed with insecticides have been demonstrated. In a study of the effects of severe DDT contamination of a colony of herring gulls in Lake Michigan, U.S.A., exceptionally high egg mortality was observed (Keith 1966). Burdick *et al.* (1964) showed that concentrations of 4.75 ppm of DDT in trout eggs resulted in high mortality of the young hatching from them. The problem of DDT and DDE causing thinning of eggshells of some species of raptorial birds is well known now, although the effect of PCB residues cannot be ignored.

Too little is known about the effects of low doses of pesticides on behaviour; published work in this area is suggestive. Warner *et al.* (1966) have shown that both organochlorine and organophosphorous insecticides can affect the learning ability of fish. Ogilvie and Anderson (1965) have shown that DDT affects temperature selection by immature Atlantic salmon, and suggested that this insecticide may interfere with the normal acclimatization mechanism.

Apart from its toxicity, the most important characteristic of a pesticide from the ecological point of view is its stability in the environment. Persistence in a toxic form is important because it allows dispersal of toxic chemicals to places far away from the site of application. Persistence also allows time for the toxic chemical to be ingested by one animal and passed to another. The extent to which this may happen depends on the ability of the organism to metabolize the pesticide. If it is able to excrete the toxic chemical quickly or break it down to harmless metabolites which may even remain in the body for some time, there will be little possibility of a harmful food chain effect. Such is the case with most organophosphorous and carbamate insecticides and also with lindane, an organochlorine insecticide. On the other hand, if the animal is unable to metabolize the chemical to harmless products and/or excrete it quickly, it will be stored in body tissues and passed to another animal and concentrated in the food chain. Of all the insecticides used for biting fly control, DDT and DDD are the most persistent and are concentrated in the food chain. An outstanding example of biological magnification of persistent insecticide was found in Clear Lake, California, where DDD was applied to the water in 1949, 1954 and 1957 at a dosage of about 14 ppb to control gnats (Hunt and Bischoff 1960). It was later found that plankton accumulated residues of 5 ppm and analysis of fish in the lake showed 40 to 250 ppm in the fat – a level high enough to cause high mortality in grebes feeding on the fish. In contrast, the use of DDD for the control of Trichoptera in the St. Lawrence River did not result in any such magnification in the food chain (Fredeen 1972). The reason may be that in Clear Lake the insecticide was used in a closed body of water whereas in the other instance it was an open river. There are other examples of biological magnification of insecticides, particularly DDT, reported in the literature. Methoxychlor, although an organochlorine insecticide and closely related to DDT in its structure, shows much less tendency to be concentrated in the food chain (Kapoor *et al.* 1970). In a model ecosystem study in the laboratory the overall concentration of methoxychlor from water at

0.00011 ppm to fish at 0.17 ppm was approximately 1500 times. In the same model ecosystem DDT was found in fish at the top of the food chain at a level of 90,000 times that of the water. However, snails appeared to concentrate DDT and methoxychlor to the same extent. This study indicated that, although the fish (mosquito fish) could excrete methoxychlor rapidly, snails were unable to do so. Further studies should be carried out to study the metabolism of methoxychlor by other aquatic animals before this compound is used on a large scale for *Simulium* control in Canada or elsewhere.

In general, concentration rates appear to be greater in aquatic systems than in terrestrial ones. This is to be expected since aquatic animals like molluscs and fish have to pass large amounts of water through their bodies to obtain oxygen and so are particularly likely to concentrate persistent pesticides. From this consideration the use of DDT or DDD as biting fly larvicides in water should be discouraged and the use of methoxychlor should be acceptable after further studies. Information about the concentration of pesticides other than organochlorine insecticides is fragmentary. Mulla (1966a) showed that the mosquito fish is capable of concentrating the organophosphorous insecticide parathion. This may be an example of exception to the generalization that organophosphorous insecticides are not concentrated in the food chain or may be the first indicator of the problem we may face in the future with the newer insecticides.

It is apparent from the above brief discussion that persistent insecticides such as DDT or DDD have great pollution potential and their use may have serious ecological consequences. The few organophosphorous insecticides discussed above represent only a small proportion of a rapidly increasing number of new larvicides available today. Information about even the most widely used organophosphorous larvicides such as Baytex, malathion, Dursban and Abate is still very patchy and incomplete; the likely impact of the other newer compounds on the environment is perhaps still a matter of conjecture. Our knowledge about the ecological impact of these newer compounds will continue to lag behind until such time as the problem is tackled in a much more systematic and coordinated manner.

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JUVENILE HORMONE ANALOGS -- THIRD GENERATION PESTICIDES?

Frank E. Strong
University of California
Davis 95616

Fifty-two years ago, when Kopec, a Polish scientist, ligated a mature gypsy moth larva and discovered that only the anterior end pupated normally, the presence of the first insect hormone (brain hormone) was established. Shortly thereafter, Fukuda demonstrated the existence of a second hormone (ecdysone), without which insects would fail to molt. In the early 1930's, Sir V. G. Wigglesworth discovered yet another insect hormone which was produced by corpra allata of immature individuals; this he named juvenile hormone (JH). After this, no major advances were made in insect endocrinology until the late 1940's when C. M. Williams at Harvard discovered that brain hormone was the trigger necessary for the release of ecdysone from the prothoracic glands. A few years later, working on a Guggenheim Fellowship in Wigglesworth's laboratory at Cambridge University, Williams found large amounts of juvenile hormone in abdomens of male cecropia moths. Upon extraction, he obtained a potent concentration of juvenile hormone. Meanwhile, in Germany, Butenandt and Karlson had succeeded in separating a few mg of pure crystalline ecdysone from 2000 pounds of silkworm pupae.

With the highly concentrated hormones available, physiologists quickly determined that they were extremely active on many varied species. Insects supplied with excess JH as larvae or pupae did not metamorphose or grew into abnormal forms incapable of reproduction. In 1955, Williams predicted that JH might become one of the most potent insecticides ever developed. However, the minute quantities then available precluded testing his hypothesis.

Years ago, Wigglesworth noted that high doses of farnesol applied topically to larvae had a juvenilizing effect. In 1965, Bowers, a USDA scientist, began testing derivatives of farnesol for JH action, and discovered that the dihydrochloride of methyl farnesoate (DMF) was 1000 times more active than the cecropia extract and suggested that pure JH would be chemically similar to DMF. One year later Law from Harvard, who also worked with terpene derivatives, discovered that simply bubbling HCl through farnesoic acid yielded an oily mixture also 1000 times as active as cecropia extract. Now, for the first time, experimenters had available enough material with sufficient activity to begin testing Williams' early prediction. In fact, Williams himself was the first to employ juvenile hormone analogs (JHA), which these materials became known as, as an insecticide. He found, in 1966, that *Aedes aegypti* larvae reared in water containing 10 ppm of Law's mixture, failed to emerge from the pupae.

The possibilities of insect control through hormonal manipulation, had now reached a feverish pitch. The Japanese found naturally occurring ecdysones in plants. Slama in Czechoslovakia discovered that DMF would sterilize the male linden bug and it could be transmitted venerally. Riddeford observed that treatment of *Oncopeltus* eggs with Law's mixture would prevent normal adult emergence. Bowers demonstrated an ovicidal effect with some of his derivatives. The current pace of discoveries has created an excitement and furor similar to that experienced by mammalian endocrinologist in the late 1920's.

Meanwhile with quiet determination, biochemists were working on the hormone structure. In 1966, a Wisconsin group, headed by Herbert Röller, announced the identification and synthesis of JH. Shortly thereafter, the structure of ecdysone was reported independently by two groups, one from Syntex Research and the other from Shering and Hoffman-LaRoche. With this knowledge, numerous laboratories quickly devised hundreds of synthetic analogs of the natural hormones. These analogs vary in biological potency, stability, penetrating power, solubility, and other factors which will eventually effect their development as commercial pesticides. Of importance, however, is that many analogs are considerably more active against selected species than the natural material. Of particular significance is the fact that the Diptera are especially sensitive to several JHA.

Around 1969, it became apparent that the potential was greater for JHA to become commercial pesticides than for ecdysones. Thus, today we find that most major pesticide firms have research teams working on JHA. Such companies as FMC, Hoffman-LaRoche, Monsanto, and Stauffer Chemical all have JHA in various stages of development. One company, Zoecon, Inc. of Palo Alto, California, was formed with the sole mission of developing and marketing insect hormone materials for insect control.

A substantial program was initiated two years ago at the University of California to evaluate the potentials of JHA for mosquito control. Working out of Fresno, Dr. Charles Schaeffer, of U.C. Berkeley has tested ZR515 (Zoecon), R20458 (Stauffer) and a Hoffman-LaRoche product, both in the lab and in small field plots. Dr. Mir Mulla, at U.C. Riverside is evaluating various JHA in southern California. At U.C. Davis, we are especially interested in the effects of the biotic factors and soil types on JHA in relation to control of *Aedes* spp. Our program is a continuation of one initiated at the University of Manitoba in 1970.

JHA are nontoxic to mosquitoes (and other insects). Applications of these materials to water containing larval mosquitoes does not interfere with feeding, growth, molting, or pupation. The detrimental effects occur when the adults attempt to emerge. With high doses, the fully formed adult will die in the pupal case. With progressively lower doses varying degrees of emergence occur before death. With very low doses, the adult may completely extricate itself from the exuvia, but dies before passing through the teneral stage.

Bioassays of JHA using mosquitoes are conducted with 10-20 selected larvae in 30-50 ml water in new unused containers. The analogs are usually applied as technical materials to the water. With such tests, concentrations as low as 0.0001 ppm have given 95% inhibition. The effective ID95 of even the best compounds however, normally does not exceed 0.01 ppm for practical purposes.

Under normal conditions, only the 4th instar is sensitive to the JHA. Treatment of 1st or 2nd instars, followed by transfer to untreated water results in no inhibition of metamorphosis. Topical treatment of eggs before the chorion darkens results in no inhibition—normal adults emerge. The pupae are especially resistant to the effects of applied JHA. This is probably due to the inability of the material to penetrate the pupal integument, rather than pupal insensitivity. Some reports have indicated that soaking pupae in high doses (100 ppm) resulted in the failure of the male genitalia to rotate. We have been unable to confirm this. We have also been unable to induce sterility by feeding adults on raisins soaked in JHA or by holding adults 5 days on moist, treated surfaces before their bloodmeal.

Very little is known about the physical chemistry of JHA when applied to water. Mostly, they are only slightly soluble, around 1 to 8 ppm. Some workers feel a surface phenomena is involved, whereby the larvae acquire an inhibiting dose only near the surface. If this is so, its impact would be important upon these species residing more toward the surface. Furthermore, we know very little about the influence of soil type on the behavior of JHA when applied to mosquito breeding sites. We do know, however, that to achieve comparable inhibition when soil is present, the dosages must be increased by 30 or more times over those needed in laboratory bioassays.

Generally, the JHA thus far studied have exhibited rather short half lives. Under sterile conditions in the laboratory, aqueous solutions have a half life in excess of 6 weeks. But under normal rearing conditions, with a high microbial count, the half life of these materials applied as emulsion concentrates ranges from 1 to 3 days. Work now underway by chemical companies and university personnel indicates that with new formulations the half life will be extended to 1 or more weeks.

The JHA have shown remarkably low toxicity to higher animals. The acute oral toxicity against rats is in excess of 5000 mg/kilo. Fish (rainbow fry) tolerated 10 ppm with no mortality. The effects of JHA on non-target species are little known, but materials which are highly effective against mosquitoes will probably exhibit lethal effects against other aquatic Diptera. I know of no tests that have been run against either Simuliids or Tabanids, but Chironomid larvae are known to be affected during mosquito control activities. The Orthoptera and Hymenoptera seem to be relatively unaffected by JHA. At Davis, our preliminary results with materials effective against mosquitoes show no effects at comparable doses on honey bees.

We now ask, "Will these JH mimics really be practical for control of biting flies? " Today the answer is a qualified "yes". High physiological activity, low mammalian and fish toxicity, rapid biodegradability are some of the characteristics of practical pesticides. Estimated production costs range from $5 to $30 per pound; if 0.1 ppm will result in control, then 0.1 pounds per acre (assuming 5" water depth) will be needed, making the cost competitive with conventional pesticides.

"When will they be commercially available? " We will probably see them available on a limited basis by the summer of 1974. There are numerous problems still to be solved, not the least of which is obtaining a label. The companies are now gathering the required toxicological data and are frantically working on large scale production methods. None of the companies has yet had sufficient material for large scale extensive field testing. Within a few months, however, sufficient material should be available for large scale testing; then and only then will we really know the future of juvenile hormone analogs.

SYSTEMS EVALUATION: ITS ROLE IN ASSESSING AND MONITORING BITING FLY RESEARCH AND IN DEVELOPING CONTROL PROCEDURES

W. O. Haufe
Canada Agriculture Research Station
Lethbridge, Alberta

INTRODUCTION

Control of biting flies and its compatability with preservation of environmental quality implies some process in management of natural systems. Therefore. ability to define, assess, and monitor change in quantitative terms becomes the major constraint for research and development irrespective either of the methods to be applied or of the complexity of the systems to be controlled. As early as 1883, Lord Kelvin stated, "I often say that when you can measure what you are talking about, and express it in numbers, you know something about it; but when you cannot measure it, when you cannot express it in numbers, your knowledge is of a meagre and unsatisfactory kind; it may be the beginning of knowledge, but you have scarcely in your thoughts advanced to the stage of science." This statement marked the beginning of a period in scientific and technical development when a concise, quantitative description of natural phenomena became the goal of physical scientists. Due either to the inherent complexity of living systems or to a traditional dependence on logic and reasoning as a more convenient approach to the study of dynamic relationships, biologists have been generally reluctant to embrace the mathematical method as a fundamental approach in research. Notwithstanding the fact that 'behavior' of cells, tissues, organs, and organisms is fundamental to all biological processes, and that this is some reason for the continuing role of reasoning in biological study, Lord Dunsany has said in reference to reasoning as the basis for scientific study, "Logic, like whiskey, loses its beneficial effect when taken in too large quantities."

I believe that assessment and monitoring in control of biting flies must be considered in the above context. For the purpose of this symposium, the essential exercise in evaluating the state of our quantitative methodology is not a matter of comprehensive accounting of new knowledge and appraisal of techniques; this has been done in a number of recent books and reviews (i.e., Southwood, 1966, Williams, 1964; Patil *et al.*, 1971). It is a matter of re-examining principles in terms of the purposes at hand, of appraising their relevance to the type of natural system to be controlled, and of projecting emphases in future research and development.

Current Status of Methodology

The importance of methodology in both research and operational work on biting flies was recognized during the early development of modern pesticides after World War II. Experimentation, however, has remained empirical, and technical and operational evaluation procedures are still largely 'ad hoc'. A notable attempt was made in 1953 by the California Mosquito Control Association Culicidology Committee to encourage a continuing investigation in the development of evaluation methods for mosquito populations (Loomis and Aarons, 1953). Thirty-seven mosquito control agencies, primarily those involved in State subvention programs, participated in the mosquito density evaluation program. The main objective was only to standardize subjective larval reports and diverse adult trapping procedures for state-wide surveys and assessments of abatement practices; but this investigation was one of very few attempts on record to develop a quantitative 'area' approach to population assessment of biting flies. For the most part, methodological assessment has received little, if any, attention in proportion to other aspects of work on biting-fly control.

Meaningful assessment of infestations for practical prediction and control must be based on representative numerical estimates of populations. Biting flies are particularly difficult to measure in this respect since population densities are confounded by considerable diversity in distributions of numbers in space and time. Few current sampling techniques meet the objective of representing numbers of individuals in a single developmental stage of the life cycle, not to mention true estimates of populations. Most ecological studies are based on the expression of a particular activity as an indication of abundance. Distributions of species are complicated by changing patterns of behavior, by developmentally distinct activities associated with different stages in life histories, and by wide-ranging dispersal of at least one free-living form in the life cycle. Biting fly systems are characteristically unmanageable from a statistical point of view either because absolute estimates are impractical in terms of resource expenditure or because practical parameters at best are only indirectly related to population levels through expression of specific activities in one or more but usually not in all life stages. Four recognized classes of estimate applied as examples to the problem of sampling mosquitoes (Table 1) illustrate the disadvantages. The first is generally impractical in terms of resource expenditure; the second is highly subjective in terms of habitat selection and may be more representative of foci in space and time than of populations or mean density/unit area; the third is usually practical in terms of resource expenditure but representative of a specific activity rather than of population numbers; and the fourth assumes at least a quasi-stability in host-parasite relationships.

A voluminous literature on biting fly research has shown little evidence of any change in direction from the 'descriptive biology' that has characterized most fields of entomology during the last two decades. A wide range of equipment, techniques and statistical methods have been developed for specific research activities in a variety of problem areas. These have been conveniently compiled in the form of a handbook by Southwood (1966) describing ecological methods pertinent to studies on animals with major emphasis on insects. An effective quantitative methodology for biting fly control, however, largely remains to be conceived and developed either from the current wealth of 'descriptive' knowledge or from new types of study embracing the mathematical method.

TABLE 1

Comparison of sampling methods for relevance as true estimates of the mosquito population

Class	Unit of measurement	Precision	Example	Parametric for population?
1. Absolute	No./unit area (geographic)	Precise in time and space	No. of eggs/acre	Yes
2. Population intensity	No./unit of habitat	Precise in time and space	No. of larvae/pool	Correlatively
3. Relative estimates	No./unit time	Precise in time only	No. adults/hr (e.g., traps)	No
4. Population indices	No. of effects, products, damages/unit area	Precise in space only	No. of animals sensitized*/1000 potential hosts	No

*Serological determination

Relevance of Concepts to a Quantitative Methodology

Success or failure of methods depends from the outset on the relevance of concepts to the systems that they are deemed to represent. Theoretical descriptions of the structure of populations have generally been approached in one of two ways, either through the principle of determinism, which is religiously considered by some biomathematicians to be the only basis for the mathematical method, or through stochastic processes. Simultaneous study of population dynamics along these two lines has always been subject to heavy debate and occasionally has culminated in severe controversy over basic parameters of measurements cf., the significance of density-dependent factors in population regulation (Thompson, 1929; Nicholson, 1933; Andrewartha and Birch, 1954). Controversial theories in the past were too oversimplified to have any serious impact on methodology in population assessments. Unfortunately, even with growing recognition of a need for generality in population concepts to accommodate the diversity of natural control of insect populations (Milne, 1957), approaches to population models have shown no change in principle. This led Richards (1961) to remark that, "Most population theories, so far as they are not purely inductive, are based on imperfect field data that are not derived from planned population studies in which all the relevant factors were measured simultaneously. In 20 to 30 years' time when more of such fundamental studies are available, we may be able to discuss our theories with more light and less heat." General lack of progress in a mathematical methodology for practical population assessment is largely due to an inability to handle complex variation that is inherent in most sampling situations. In this connection, especially, biting flies with their broad diversity of habits and habitats are commonly avoided in fundamental studies in population dynamics.

Continuing efforts to develop sound sampling systems for studies in population dynamics have produced some useful guidelines and methods in biostatistics (Patil *et al.*, 1971a, b). The sequential sampling procedure (Oakland, 1950; Morris, 1960) was one of several improvements in assessing pest density in relation to control measures in which operations are contingent on the criterion that the pest density has reached a certain empirical level. The number of samples taken in this case is variable and depends on whether or not the results obtained at any given stage in the operation give a reliable estimate of the frequency of occurrence of an event (i.e., abundance of an insect). Extensive preliminary work, however, must be done on an individual species to establish not only its distribution but also the generality of a precise type of model in accommodating the diversity of environments to be encountered. In many cases, statistical parameters change with density so that most sampling methods and their related analytical procedures are limited to specific problems or to particular types of environment. All popular applied biostatistical analyses and procedures are empirically based on probabilities and, for this reason, have to depend primarily on informed assumptions of how much is known about the life cycle, habits and distribution of the species concerned. Procedures and methods are useful if the resource input (work involved in sampling) is practical in relation to information returned for a given level of confidence in the adequacy of available knowledge. Overwhelming diversity in the nature of insect dispersal has been the major obstacle to practical adoption of this type of biostatistical approach in studies of blood-sucking flies. Johnson's comprehensive treatment of the displacement of insects (1969) has informatively documented the concept that assessment of airborne populations involves a high magnitude of environmental interaction. Biting flies in particular present additional difficulty in quantitative assessment of infestation levels since migratory displacements described by Johnson for certain groups of insects such as aphids are unlikely to be as important or as common in the behavioral patterns of hematophagous species.

The life table has been emphasized by some ecologists as an important entomological innovation in understanding the population dynamics of a species (Deevey, 1947). Because insects tend to have discrete generations and their populations are rarely stationary, the age-specific life table which is based on members of a population belonging to a single generation has greater application in economic entomology than the time-specific one which is based on a sampling of age classes at discrete points in time. Some tables have been constructed with estimates of absolute populations at different stages and combined with related records of known mortality factors to form what is more aptly designated as a population 'budget' (Richards, 1961). The difficulty in accounting for population changes with this type of assessment is in having access to all or at least most of the life stages for sampling purposes. In this respect, the possibility for example of extracting eggs from soil as valid samples of a stable stage in the life cycle of mosquitoes is not very promising in terms of monitoring populations in biostatistically acceptable unit areas within reasonable limits of expending resources. Moreover, egg density, which is the most significant single sampling estimate for population potential in a life table or 'budget', is still a very imperfect parameter of infestation potential for biting flies. In temperate climates, it is critically subject to the phenomena of 'arrested development' which ensures survival of the species; hence, depending on weather, it too can be an extremely variable parameter of the 'fly infestation' for seasonal generations. Estimation of numbers of reproductive adults as an alternative measure of predictive importance offers less promise with the techniques available so far. In most cases, quantitative assessments are complicated by atmospheric displacement of the majority of individuals in populations. Precision is an elusive objective in sampling any single stage in the cycle of biting flies as a parameter of economically important infestations.

Future Emphases in Quantitative Methodology

Potential in research and development in any field of study usually depends on a combination of (1) an effective and systematic organization of resources (current work input) and (2) technical innovation from the existing pool of scientific and technical knowledge. On the basis of these two criteria, it is possible to project some new approaches to an evaluation of control systems for biting flies.

A considerable knowledge of biting flies has been accumulated and more is continuing to be developed in the traditionally descriptive form of natural history, function, and bionomics of species. Because of diverse habits and distributions associated with biting fly life cycles, increasing emphasis and effort must be directed to the elucidation of systems relating to reproduction, to habitat selection and related aspects of environmental infestation, and to host attraction. These must be considered as interdependent processes in the main problem of dispersal and displacement of populations. Stochastic processes in modelling are more likely to form useful bases for systems evaluation in this respect than the conventionally rigorous deterministic models in classical mathematical methods. Mathematical models, by their nature, over-simplify and hence distort complex interacting systems that they are intended to simulate. This is particularly true of deterministic models and it is essential that the assumptions made are clearly defined in terms that are relevant to the system studied. Stochastic models are more adaptable to discrete sub-systems which, once designed and validated by experiment, can be integrated and easily modified, if necessary, to simulate progressively larger natural systems as capabilities develop in research and technical activities.

It is obvious that to evaluate biting fly control, the mathematical method and related quantitative attempts to model real systems for the purpose of assessment and monitoring must be clearly oriented to the problem of adult dispersal. Atmospheric displacement and its relation to breeding sources is the key system to be elucidated, defined, and validated for any management or development scheme irrespective of its dependence on chemical, integrated, or any other type of control. Biostatistical methods have a continuing practical role in the evaluation of discrete mechanisms governing integral physiological and ecological processes; but a new strategy of assessment must be based on operational models of more complete systems or functional sub-systems. The modelling process in this case must have a built-in system of continuous assessment containing clearly specified criteria which are relevant to equally clearly specified objectives for the management or control of the natural system, i.e., control of biting flies. This implies primarily that continuing studies be justified by 'deeds' (in terms of technical control or management of the 'fly' system) rather than by 'words'. The point is that simply acquiring data on any system, mechanical or natural, and subjecting mechanisms to endless tests of precision will not lead automatically to the kind of understanding that enables knowledgeable control or management.

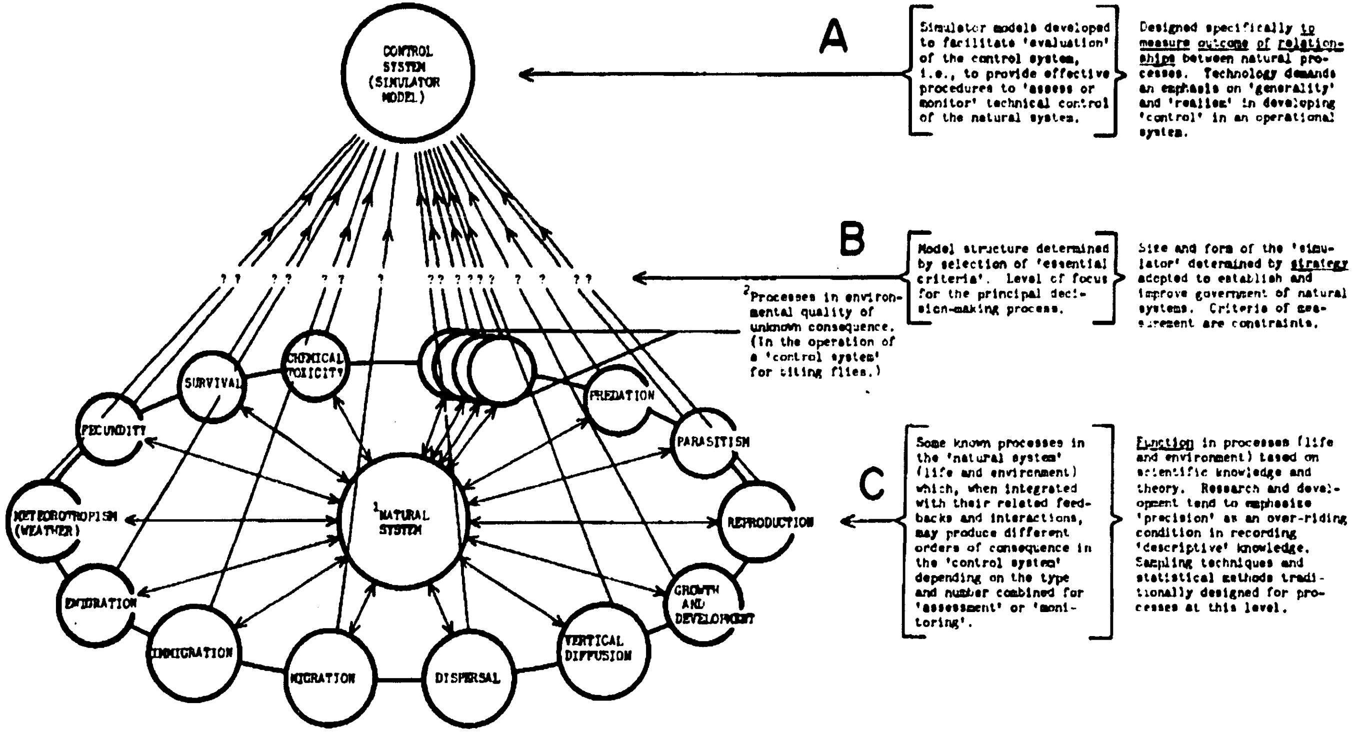
Systems Analysis and Model Building

The purposes of assessment and monitoring in abatement of biting flies are served most appropriately in a simulation of the particular natural systems that we wish to control. The problem is more fundamental than the development of efficiency and sophistication in sampling techniques, analytical methods, and biostatistical procedures. It is posed by the fact that, in spite of the vast amount of descriptive knowledge available on biting flies, we are unable to state the relevant biological phenomena (processes) in a quantitative manner so that we may exploit existing mathematical methodology in its fullest capacity. It is important to note that processes, not structure, characterize the system. The aim is to seek appropriate degrees of realism, generality, and precision in the systems model (Levins, 1966). Since these three characteristics tend to be mutually exclusive, a compromise has to be struck at successive stages of development and evaluation in terms of the intended function of the model.

If the two criteria already stated are valid for increasing potential returns in research and development, it is possible in general terms to conceive key processes, such as dispersal from breeding areas and atmospheric displacement, as integral parts of a simulator model for control of biting flies in a natural environmental system. The utility of a 'simulator' as a working tool in either research or development depends essentially on a distinction in the conception of the 'model' between scientific and purely mathematical strategies (i.e., between stochastic and deterministic processes). It requires selection of the essential criteria to achieve acceptable levels of practical correspondence between 'control' and 'natural' systems (Fig. 1). Simulators are usually conceived to have their own feedback systems so that the model becomes self-regulatory and is programmed to mimic the system after which it has been designed. The perfect numerical simulator in this case would be expected to have its own system of feedbacks (to be added at Level A, Fig. 1) which mathematically mirrors the natural system of biological processes (Level C, Fig. 1). This concept is undoubtedly idealistic and too complex to contemplate from the point of view of practical operations. It is the type of concept that would have to be considered in the ultimate 'management' of pest populations on a large geographic scale; but it is unnecessarily sophisticated for the purpose of assessing or monitoring progress in a biting fly control program in the present state of our knowledge. Therefore, there is an important immediate need now to measure the indicators directly related to the practical outcome expected in control programs. These measurements must be simulated essentially in the form of integrative processes (Level A, Fig. 1) for the purpose only of evaluating progress in technical capability. Decision making and judgment in scientific and technical activities are essential in the continuous evaluation of the control system (Level B, Fig. 1). They depend on the ability of scientists and technologists to select appropriate natural processes (Level C, Fig. 1), the minimum number of which are likely to provide assessments with acceptable limits of confidence on the basis of current knowledge and capability. Much of the activity in assessing even relatively uncomplicated systems such as control operations with synthetic chemicals must continue to be largely trial and error with a one-way input at the decision-making level (B). Meaningful practices in assessment, however, must begin to reflect simulator design with some relevance to practical affairs as defined in living systems. They must involve function in processes, strategy in structure, and a clearer picture of the outcome of interactions in integration. Shortcomings in research and development, if they are to be pointed out for control of biting flies, have to be expressed as a lack of assessment so far in terms of strategy and outcome of interactions, both of which contribute to 'effectiveness' as distinguished from 'efficacy'.

Organization of Simulator Systems

There is no limit to the size of a system (Miller, 1965). Therefore, the amount of functional organization of available scientific resources and technical capacities to achieve control in the simulator model determines the practical size and structure of the system to be simulated and evaluated. The objective may involve any number of interrelated sub-systems conceived as integral parts of the ultimate system. If 'dispersal of biting flies' is considered as the ultimate or some penultimate to antepenultimate stage of the systems simulation, then sub-systems might be associated with processes already elucidated such as hygrothermal conditioning of flight activity in mosquitoes (Fig. 2) (Haufe, 1966). Vertical distribution, migratory displacement, emigration, immigration, emergence, and diel cycling of activity are a few other relevant processes already described for various insects (Johnson, 1969). When compounded, these processes obey the natural laws appropriate to a collective system that is quite different from that of the individual organism in experiments. Therefore,



A: Simulator models developed to facilitate 'evaluation' of the control system, i.e., to provide effective procedures to 'assess or monitor' technical control of the natural system.

Designed specifically to measure outcome of relationships between natural processes. Technology demands an emphasis on 'generality' and 'realism' in developing 'control' in an operational system.

B: Model structure determined by selection of 'essential criteria'. Level of focus for the principal decision-making process.

Size and form of the 'simulator' determined by strategy adopted to establish and improve government of natural systems. Criteria of measurement are constraints.

[2]Processes in environmental quality of unknown consequence. (In the operation of a 'control system' for biting flies.)

C: Some known processes in the 'natural system' (life and environment) which, when integrated with their related feedbacks and interactions, may produce different orders of consequence in the 'control system' depending on the type and number combined for 'assessment' or 'monitoring'.

Function in processes (life and environment) based on scientific knowledge and theory. Research and development tend to emphasize 'precision' as an over-riding condition in recording 'descriptive' knowledge. Sampling techniques and statistical methods traditionally designed for processes at this level.

[1]Natural system conceived to embrace development, reproduction and dispersal in populations.
[2]Processes in environmental quality include pollution (soil, air, water), energy transfer, nutrient transfer, chemical degradation, etc.

Fig. 1. Simulation of 'control' and 'natural' systems and its relation to the problem of assessing and monitoring effectiveness under the influence of essential life processes in the environment.

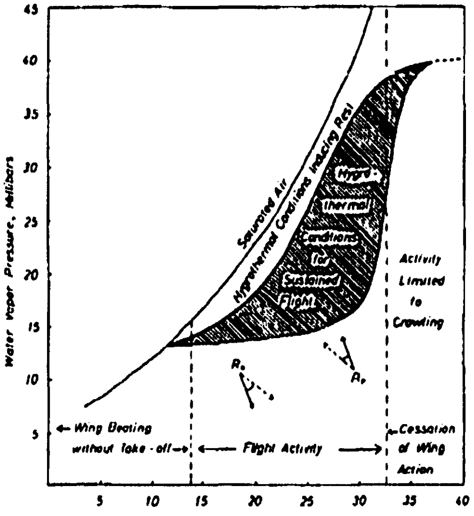


Fig. 2. A psychrometric diagram of response to hygrothermal conditions which represents meteorotropism as one of the processes contributing to an integrated model for numbers of active mosquitoes.

the decision on the size of the system to be evaluated with the resources available depends initially on an organizational capacity to identify the most essential component processes for the purposes at hand. The next step is to structure the system as a simulator model in which 'control' can be evaluated for purposes of either research or development. The main advantage in assessment procedures based on this principle is that serious gaps in our knowledge of relevant processes become apparent immediately; in the same manner redundancy of certain types of 'descriptive' work is identified and eliminated in favour of more essential requirements. Successive evaluations and tests of the system must always contribute to improvement in system control and related scientific and technical capacity.

The main implication in the organizational structure for this approach is that the majority of workers would have to be attuned to the role of identifying key processes in the natural systems with which they are associated. The customary individualized approach to science and technology would have to give way to organized collective programs focused conscientiously on the key natural systems.

Technical Innovation

Implementing an organization of simulators for assessment of biological systems such as dispersal of biting flies would depend on two technical capacities. One of these must accommodate an automatic sampling operation for the minimum initial complex of processes included in the model; the other must facilitate mathematical methods in the statistical and structural assessment of combined processes in predicting, testing, and controlling the system.

Since comprehensive simultaneous modelling of several processes compensates for reduced precision in the individual components, it is theoretically possible to dispense with a specification of absolute samples in favour of relative estimates based on activity. This option has a logistic advantage since new electronic capabilities offer limitless possibilities to the innovative technician. For example, automatic electronic counters and recorders for flying insects contacting an attractive surface or entering a standard air space are all technically possible to equip large-scale realistic simulators in outdoor laboratories. The compromise in this case is advantageous for the purpose at hand since a model designed to test alternatives in control (or management) of the natural system generally sacrifices precision to gain realism and generality. From this point of view, sampling requirements may be met with modest resources that are appropriately organized and allocated.

In the case of the second requirement, biologists have failed to capitalize on the powerful techniques already available in mathematics and computer science. The current knowledge in these fields far exceeds our capability to articulate relevant biological processes in a quantitative form. Humble beginnings, however, are being made in simple simulator models for biological application. Some of these have already been directed to the general problem of dispersal of animals among units of discrete habitats, a process fundamental to natural population systems (Kitching, 1971).

For the traditional biologist, initial exposure to the systems approach conjures up a formidable mathematical methodology to which he is not attuned and for which he feels an inability to master. Nevertheless, the main problems will continue to be biological rather than mathematical or computational, since keen biological insight will be necessary to define the processes in a meaningful way and to design structures to relate them in control systems. In this case, powerful computer techniques may not have to be adopted necessarily in the form of highly involved mathematical matrixes. Graphic forms of simulator models are already the subject of serious study (Pitteway, 1972). Early algorithms were prohibitively slow with required computer time varying as N^2 where N is the number of objects to be processed. Recently, pictures of increasing complexity are being processed with greater speed and efficiency and have included the calculation of processes varying from the Fourier transforms to the sorting of trees. It is not difficult, for example, to conceive of a perspective computer drawing of mathematical surfaces (Fig. 3) as a three-dimensional representation of mosquito abundance for automated electronically instrumented geographic areas as mentioned earlier. One picture in this case is potentially more informative as part of the systems approach than thousands of words from traditional descriptive biology. Moreover, where related processes such as vertical distribution of mosquitoes and atmospheric circulation are linked by computer plots in appropriate time series, *we are beginning to assess the functional relationships that govern outcomes of natural systems*. When the traditional biologist discovers the art of this new type of quantitative methodology he will undoubtedly be less apprehensive of the mathematical approach as advanced by computer sciences. We are more likely also to be achieving the real objectives of our research and development activities.

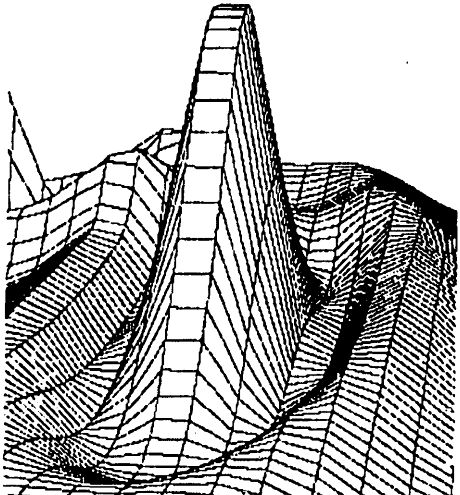


Fig. 3. A computer drawn surface.

SUMMARY

A systems approach is considered to be the only promising option open to research and development for an advance in control of biting flies. Sophistication of quantitative methods of assessing, monitoring, or testing control and management is best achieved with modern techniques as an integral part of a simulator model combining essential biological processes as characteristics of natural systems. The objective should be to develop functional models which assess *functional relationships that govern outcomes* of natural systems instead of continuing to produce descriptive models which assess *precision in measuring outcomes of function* in natural systems. This change in emphasis depends on the adoption of a strategy that converges on control (or management) capability.

Some implications for developing a more effective quantitative methodology in the new approach are:

(1) Simulator models must be isomorphic in terms of control strategy so that sub-systems may be individually tested and evaluated for successive integrations into larger manageable systems.

(2) Relevant biological phenomena or processes must be articulated in quantitative terms to embrace the technical advantages generated by mathematics and computer science.

(3) Some of the precision traditionally demanded in the *description* of function must be compromised for generality and realism in simulator models to facilitate appreciable measures of control in the natural systems.

(4) Essential processes as represented by subsystems must be identified at each stage of development in expanding control of the system.

(5) Emphasis on 'descriptive' work will have to be reduced in order to sustain an increased effort in identifying essential relational structures of processes for integration.

(6) The practice of 'learning all about' mechanisms has to be replaced by incisive investigation of essential processes to facilitate the integrative evaluation of the 'control' function in the system. This is to say that 'research' strategy as well as 'development' strategy is aimed directly at control and from the outset employs modern principles of control theory.

(7) Collectivized rather than individualized approaches in research will be necessary to obtain 'effectiveness' and to converge on the common goal of capability in controlling natural systems.

(8) The mathematician is concerned with generality in the form of a statement; the scientists with generality in its content. The first generality is one of language and the second one of fact. Therefore, the mathematical method, insofar as biological assessment is concerned, has potential advantages for precision and conciseness in 'control' systems. These potential advantages, however, will not produce tangible benefits unless they are exploited in accordance with scientific rather than purely mathematical strategies. Until 'model' makers learn this lesson, the 'mathematical simulator' seems likely to remain an art form rather than a working tool for such socioeconomic problems as control of biting flies and management of the environment.

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NEW APPROACHES FOR MARK-RELEASE-RECAPTURE STUDIES OF BITING INSECTS

G. A. H. McClelland[1], Robert J. McKenna[1] and Thomas A. Cahill[2]
Departments of Entomology[1] and Physics[2]
University of California
Davis, California

INTRODUCTION

The need to preserve environmental quality has encouraged the search for alternate means of biting fly control that do not involve the indiscriminate application of chemical pesticides. Although biological control and autocidal methods involving mass release of insects may not be generally practical under Canadian conditions, they merit consideration under special circumstances.

The effect of a mass release is strongly inversely dependent on the density of the natural target population in sharp contrast to the density independent effect of chemicals.

Proposed use of any autocidal or predator release method against a population of biting flies thus requires a knowledge of its density and dynamics that has hitherto been generally lacking.

One of the most powerful tools for estimating absolute parameters of natural populations of animals involves the release and recapture of marked individuals. Statistically ideal methods require the following assumptions:

1. Animals are not affected by marks;
2. Released animals mix with the general population;
3. The population is sampled randomly with respect to age and position in the habitat; and
4. The marked animal has the same probability of capture as the unmarked.

All marks probably affect an insect in some way, so the ideal is probably unattainable. Tests can however show if the effect on survival is significant or not and marked individuals should be observed feeding and ovipositing in typical fashion.

Female mosquitoes and other biting insects demonstrate a gonotrophic cycle with a period of about 3 days. The phase of this cycle profoundly alters behavior, especially feeding and oviposition. Superimposed on the gonotrophic periodicity of behavior are usually well defined circadian periodicities. The simultaneous presence in a population of different behavioral phases can severely interfere with the other ideals of the mark-release-recapture method. For example, a replete, blood-engorged, mosquito may not only show a reluctance to fly, but may rest in a different place from one that is gravid or one that is empty and hungry. No method seems known which would sample all behavioral phases with equal probability. If catch samples were biassed to one or more phases of a physiological cycle it follows that the marked and unmarked individuals would not be at equal risk in the population. The hungry mosquitoes caught and marked yesterday would have fed and be less likely to be recaptured today, whereas yesterday's gravid mosquitoes which eluded capture would today be seeking a meal and probably more readily caught.

Since the physiology of natural populations cannot be controlled, the cyclic changes that exist can, at best, be exploited by sampling insects in a particular phase, and that phase alone. Thus

McClelland and Conway (1970) caught mosquitoes coming to feed and only released fully engorged females. Not only was the normal activity pattern little modified, but the released mosquitoes, in theory, would pass through the complete cycle before being at risk of recapture. Since this would involve their seeking an oviposition site and returning to feed again, opportunities for population mixing through normal behavior were increased. Analysis of this type of data (Conway, Trpis and McClelland, in press) is more complex since probability of recapture no longer declines steadily from the date of release but shows the modality of the physiological cycle. This in itself is valuable as, more important in the case of biting insects, it allows the direct estimation of frequency of blood feeding (McClelland and Conway, 1970) and hence vector potential.

The simplest experiments based on the Lincoln Index require only a single release of marked animals but they do not permit estimation of life-table or dispersion parameters. More sophisticated designs call for a series of marking occasions (Fisher and Ford, 1947; Bailey, 1952; Jolly, 1965) and, for dispersion estimates, a series of release sites. A design calling for 10 consecutive releases from 10 different sites thus needs 100 different marks.

Large animals and even large insects offer fewer problems for multiple marking. Dr. Norman Gary of Davis has for example glued numbered metal disks to bees and such a method might be extended to large biting flies such as tabanids or *Glossina*. Working with small populations of yellow fever mosquito, Sheppard *et al.* (1969) in Thailand and McClelland and Conway (1970) in Tanzania were able to hand-paint number codes on individual mosquitoes, because single-day catches were less than 50. In these cases high recapture rates provided adequate data from the small samples.

The dense and extensive populations of many mosquitoes, particularly those of lakes and floodwaters and of most of the biting insects of Canada, preclude individual handling. Marks need to be applied quickly to large numbers of insects en masse in order to yield a useful number of recaptures. Known marking substances, however applied, fall into three groups: radioactive trace elements, dyes and fluorescent dusts (Southwood, 1966). All three have the serious limitation that the number of clearly distinguishable marks is, most optimistically, below ten. Radioisotopes suitable for marking live insects have the disadvantage of short half-life. Neither dyes nor isotopes can be identified without special treatment. An entire catch must be processed with solvent or taped to X-ray film in order to recognize a possibly minute proportion of recaptures. Fluorescent dusts have been widely used and have the great advantage, over radioisotopes and dyes, in that marked insects can be recognized alive by brief exposure to ultra violet light. Unmarked mosquitoes in the catch can thus be marked and released to increase the efficiency of the operation. Again the number of dusts that fluoresce well and are distinguishable is less than ten.

METHODS AND DISCUSSION

Rationale

The analytical method used in the present study owes its development to the improvement of techniques for detecting trace contaminants as indicators of atmospheric pollution. Thus, it has also indirectly risen from the need to preserve environmental quality.

Minute quantities of heavier trace elements can be detected and identified by their characteristic X-ray emission spectra when bombarded by alpha particles or an electron beam. Suitable trace-element compounds can thus be added to a fluorescent marking dust in various code combinations. Such elements must 1) not be detected in unmarked insects, 2) be insoluble, stable and unreactive, 3) produce identifiable X-ray spectra in the presence of X-ray emission from the other marker elements, natural elements present in the specimen and that from the marker dust. Possible trace element compounds are listed in Table 1 in ascending order of approximate price.

Table 2 lists the number of different code combinations generated by using a different number of elements out of a given number of candidates. The addition of a constant number of elements provides a parity check against missed identifications but if all combinations are used the number of codes available is much greater. Where zinc sulfide is used as the visual marker its presence is confirmed by its X-ray spectrum. Naturally occurring fluorescence such as reported by Reeves *et al.* (1948) thus can cause no problem.

TABLE 1

Candidate trace elements or compounds for marking

Compound	Relative price ($/25 gms)		Relative price ($/25 gms)
1 Zirconium Oxide	1	8 Cerium Oxide	4
2 Tellurium Oxide	2	9 Selenium	5
3 Molybdenum	2	10 Niobium Oxide	7
4 Bismuth	3	11 Tin	10
5 Thorium Oxide	3	12 Indium	25
6 Lead	3	13 Uranium Oxide	26
7 Lanthanum Carbonate	3	14 Silver Oxide	26

TABLE 2

Number of possible code combinations for trace element marking

	No. different trace elements					
No. used together	5	6	7	8	9	10
1	5	6	7	8	9	10
2	10	15	21	28	36	45
3	10	20	35	56	84	120
4	5	15	35	70	126	210
5	1	6	21	56	126	252

Procedure

Mosquitoes are dusted with a mixture of the zinc sulfide powder found to be brightest by Bailey *et al.* (1962), Helecon® no. 1953, and the appropriate trace elements, each in an atomic ratio of about 1:100 to the zinc. This ratio was found by preliminary tests to be the minimum for reliable detection. However, some elements which have a lower probability of X-ray emission must be added at higher proportions.

For decoding, marked mosquitoes are killed and fixed on sheets of .25 mil mylar® film. Protected in this way they can be kept indefinitely since the atoms are completely stable. Field work and code analysis can thus be conveniently separated in space and time yet the progress of an experiment is known immediately from the recapture rate. Although trace-element analysis of an individual mosquito is relatively costly and requires the facilities of a cyclotron, it should be remembered that only known recaptures are tested, so no time or money need be wasted on unmarked insects.

When the samples are ready for testing at the cyclotron they are mounted on a rotatable target wheel or other sample changing device, inside a vacuum chamber in the path of a focussed-beam of alpha particles generated by the cyclotron. All the atoms in the path of the beam emit X-rays. Each element produces a characteristic spectrum which peaks at certain energies. The X-rays are detected by a silicon/lithium device and the photon counts of X-rays at each energy are integrated through time by an on-line computer which can also control the duration of counting until all marks are discriminated. The longer the sample is analyzed the better the different energy peaks can be distinguished from background noise. Futhermore, since the process is non-destructive, the same sample can be analyzed again if initial results are equivocal. Fig. 1 shows a typical spectrum of a marked mosquito. The lighter elements, Hydrogen, Carbon, Oxygen, Nitrogen, Sodium, Calcium etc., naturally occurring in the insect tissue and the zinc of the marker dust generate a lot of lower energy X-rays. The higher energy part of the spectrum however is largely empty save for system noise and the trace element spectra. Sensitivity can be improved by the use of appropriate filters to cut down unwanted parts of the spectrum.

Although our technique has not yet been tested in the field, published data for trials using zinc sulfide dusts alone are extensive (Southwood, 1966). The small amount of each compound needed relative to the zinc sulfide dust, and the non-reactive nature of our candidate substances, suggest that these compounds would not greatly alter behavior or increase mortality. The preliminary results from our survival studies tend to verify this suggestion.

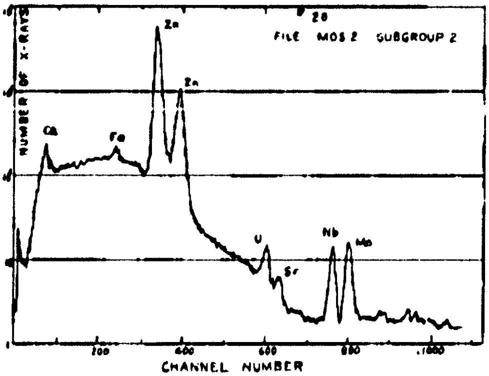

Fig. 1. X-ray fluorescent spectrum of mosquitoes dusted with zinc sulfide and trace quantities of Uranium, Niobium and Molybdenum.

Although there was some difference in survival between unmarked controls and dusted treatments, there seems to be no significant difference (at the 5 percent level) between the treatments with zinc sulfide only and those using trace elements in addition. Attempted feeding and oviposition has been observed in all test groups, suggesting that tagging interferes little with behavior.

SUMMARY

Two new approaches to mark-release-recapture studies of biting insects are suggested.

1. The selective sampling of a particular physiological phase.
2. The use of fluorescent dust together with trace elements to permit mass-marking with a large number of distinct codes.

The method is appropriate for extended field use in remote areas.

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DISCUSSION

Discussion Leader . . . . .R. Frank
Discussants . . . . .C. R. Harris
M. S. Mulla

Frank: This morning Drs. Provost and Hocking very ably defined the problems of 'biting' flies in human society. These pests not only cause annoyance to man and his domesticated animals, but also cause human distress and the death of livestock. Dr. Provost pointed out that 'biological man wants to control biting flies but rational man also wants environmental quality and reconciliation becomes the order of the day'.

Each speaker outlined guidelines on the approach to biting fly control that, if integrated, could rationalize our approach to the problem. Dr. Provost felt that the environment was made up of several components each requiring different degrees of control. His categories were the home (indoors), the home surroundings, and the urban, rural and wild environments. Dr. Hocking felt that the approach to biting flies could be pursued down three avenues, fly population control (larva or/and adult), personal protection, or an integration of the two methods. The 'biting' fly pests in Canada were primarily mosquitoes, blackfly and tabanids. It was lamentable to hear of promising programs that had been terminated over the years since the late forties (see Dr. Hocking's paper).

A few speakers referred to some basic studies but most involved applied research. Traditionally man has attempted to control his pests without first conducting basic studies into the behaviour of the pest and the pest-predator-parasite relationships. Only now is research being carried out in agriculture to integrate natural and technological control methods. It would appear that much work is needed on basic studies into the behaviour of biting flies.

The biting flies of northern Canada might be looked upon as 'protectors' of the environment. They have effectively prevented man's invasion of the wilderness and in so doing have helped to preserve the natural environment. The tsetse fly of Africa can also be credited with preserving the sanctuary and the lives of many wild mammals that would have otherwise become extinct.

Chemical control presents a short term method for fly population control on small areas at relatively low cost. Unfortunately, all too often the short term benefits do not outweigh the long term costs. There were two speeches on this topic and it is evident that we still adhere to a 'squirt and look' philosophy. The aquatic environment is probably the most delicately balanced of all environments and is therefore the most easily disturbed. More study is required into the impact on non-target organisms when chemicals are introduced into water. Studies are all too frequently conducted on single organisms of the system but rarely on the system as a whole. It should be pointed out that systems vary considerably from location to location. As noted in Dr. Saha's paper, pH of the water has a profound effect on the rate of degradation of organophosphorous compounds. In Northern Ontario with the fallout of sulfur compounds, the pH of many lakes has dropped from 5.5 to about 4.0 in a matter of 10 years. This in itself would greatly change the degradation rate of an introduced chemical insecticide.

I shudder at the use of DDT on particulate matter especially in the northern areas where water is pristine, cold, and often flows through deep lakes. Experience in Ontario shows that the use of only minute quantities of DDT in the Muskoka Lakes or James Bay has resulted in persistent residues that are predicted to remain for long periods. In the warmer, polluted rivers of Southern Ontario where large scale use of DDT has occurred over land, residues appear to be degraded rapidly and even recently applied DDT is already largely degraded to its metabolites. Use in the northern region of the Province has been mainly over rocky surfaces where most finds its way into the aquatic environment and appears little changed in 5 years. In the southern area, the major portion used is held by soil and converted to DDE and only finds its way into the aquatic environment when soil is eroded. Laboratory studies reveal that chemical pesticides applied to polluted water are more rapidly degraded than those applied to cold, pristine water (e.g. 2,4-D). Hence care must be taken in assessing degradation under field conditions and extrapolating it to the general environment.

Dr. Strong outlined the advances made in the use of juvenile hormone analogs for biting fly control. The specificity of these compounds would indicate that the number of non-target organisms that could possibly be affected would be few compared to the numbers affected by the broad spectrum insecticides.

As a rational approach to biting fly control, I propose the following scheme as a guideline:

1. *In the home* – The need here is for complete eradication. The approach would include the use of screens to prevent entry of insects and insecticides to kill those that did gain entry; DDT might well have a place in this situation. These will, by necessity, be adulticides and will not impair public health.

2. *The home surroundings and the urban environment* – These environments are managed and controlled by man; hence, more rigorous methods of control are possible. Here mechanical, chemical and biological control might be undertaken in an attempt to eradicate fly populations. The nearness to human habitation will mean adulticides will make up the backbone of the insecticides used. Some use for larvicides can be made in non-drinking water.

3. *The rural environment* – The area is much too large to attempt eradication. Hence a less rigorous system of integrated control by cultural, mechanical, chemical and biological methods should be made. In rural areas surrounding urban centres, larviciding will probably be of considerable value, adulticiding will largely be used for clearing space of biting flies around dwellings.

4. *Wilderness environment* – If the wilderness is to be preserved as long as possible, it seems inadvisable to larvicide or adulticide in these areas. The area is huge, the cost would be enormous, and the result would be to bring this environment under man's management. It would appear that personal protection is the most desirable approach to the problem. Local adulticiding programs in the immediate environment of humans at work or at sleep is acceptable.

The use of repellents, protection kits, and possible sex attraction traps could be further investigated for wilderness use. It would appear better to protect man from the biting fly and thus preserve the wilderness than to subjugate the wilderness by controlling biting flies.

The degree of control of biting flies should vary according to the habitat from a policy of eradication in the home to a policy of personal protection in the wilderness environment.

Harris: It is apparent from the papers given in this Section of the Symposium and in those to be given in subsequent Sections during the next 2 days that research in biting fly control is moving ahead on several fronts, i.e. chemical, cultural, and biological control, and personal protection. Exciting advances are being made, particularly in the area of "biological control." However, one point is very noteworthy, i.e. most speakers including those involved in biological control have made reference to the fact that these newer techniques will, of necessity, have to be integrated with some form of chemical control.

The fact is, that chemical control of biting flies will remain in the forefront for many years to come. Thus, exciting as the new approaches to biting fly control may be, we must continue to give equal priority and emphasis to research on the control of biting flies by chemicals. Unfortunately in Canada, this area of research is being sadly neglected.

In the past, in Canada, biting flies were controlled with the organochlorine insecticides, particularly DDT. I am sure that everyone here is aware of the environmental problems which have arisen as a result of the extensive use of DDT and I need not dwell on them to any great extent. However, I was concerned with comments made by several of the speakers today in which they tended to shift major responsibility for DDT pollution on to its extensive use in agriculture and forestry. For example, Dr. Provost, stated that "Possessed of a miraculous tool in DDT, disregarding numerous warnings, man proceeded to use it recklessly, killing their natural enemies along with the pests and generally ignoring the biosphere and man's place in it. Although this charge can be more deservedly levelled against farm and forest use of DDT, the control of biting insects was far from blameless." To this last statement I must take exception. Certainly agriculture and forestry have contributed to the DDT problem. But, for prime examples of reckless use of DDT in Canada, one must only look at the biting fly control picture over the past 2 decades to realize what uncontrolled use of insecticides can do. For example, in Ontario, DDT has been used extensively in the tobacco-growing areas for many years, primarily for cutworm control. Residues in these light, sandy soils average 3.2 ppm. DDT was used up to and including the year 1971 until satisfactory replacement insecticides were registered for use. This area of approximately 100,000 acres lies within the Big Creek watershed which drains into Lake Erie. For several years, Mr. J. R. W. Miles of our staff has been monitoring DDT residues in water in Big Creek. His information indicates that in 1971 an average of 2/10 of a pound of DDT/wk entered Lake Erie from Big Creek. By contrast, in the Muskoka resort area of Ontario, DDT was used extensively for biting fly control up to 1966 and officially has not been used since then. A study by Mr. Miles in 1971 showed that DDT entering Lake Huron via the Muskoka river system averaged 2 lbs/wk. In other words, the use of DDT for biting fly control in this resort area up to 1966 was still contributing 10x the amount of DDT as compared to the tobacco-growing areas where this material was still in use in 1971. Other studies have shown that residues in fish in Lake Erie are much lower than those found in fish in Lake Huron. Clearly, in Ontario at least, and I suspect elsewhere in Canada, the use of DDT for biting fly control has been a major contributor to the problem of DDT pollution of the environment.

Because of the environmental problems caused by some organochlorine insecticides, drastic steps have been taken to restrict their use, and substitute other compounds. At present, these substitute materials, with the exception of methoxychlor, are either organophosphorus or carbamate insecticides. A number have been mentioned by Drs. West and Saha today which are either being recommended for use, or show promise in experimental studies, e.g. malathion, Abate (R), chlorpyrifos, fenthion, Baygon (R), dichlorvos, carbofuran, and several others. In addition, as discussed by Dr. Strong, another group of chemicals, the juvenile hormone analogs also show promise in experimental laboratory and small scale field programs. It is encouraging that effective alternative chemicals are being found. However, it is discouraging to note the rather off-hand approach which researchers are taking with regard to the persistence and metabolism of these newer organophosphorus and carbamate compounds in the environment and their potential side effects. It is a common assumption that the new insecticides are easily biodegradable and thus will not result in any unwanted side effects. However, the facts are that we have very little information on the persistence, metabolism, or side effects of any of these compounds, particularly under Canadian conditions. Procedures for extraction, cleanup, and analysis are, in most instances, inadequate. Experience in agriculture and forestry has already shown that some of these compounds are more persistent than expected, that some are metabolized to other toxic and more persistent metabolites in soil, and that some also markedly effect non-target organisms. There is no reason to believe that the situation will be any different when it comes to biting fly control. The situation with juvenile hormone analogues is similar. It must be remembered that these are basically organic compounds, and the questions raised with the organophosphorus and carbamate insecticides apply equally well to this new group of organic chemicals.

In concluding my remarks, I would like to reiterate my statement that organic insecticides will remain in the forefront for biting fly control for many years to come, and I would like to put forward the following suggestions:

1) That, in Canada, financial support of the biting fly research program should give equal consideration to the development of effective chemical insecticides as to other promising approaches to control such as biological control and personal protection.

2) That major consideration be given not only to finding effective chemicals and formulations, but also to determining the fate of these compounds under Canadian conditions. There is virtually no work of this nature underway at the present time.

3) That effective legislation, based on sound scientific reasoning, rather than political consideration, be developed to control the use of insecticides used for biting fly control.

Mulla: As a discussant, I am allowed about ten minutes to present my remarks on the contents and subject matter of the papers presented today by a group of scholars and scientists, each one of whom have attained world renown in their field of interest. It therefore will be difficult for me to add anything significant to what has already been said and discussed here today. I will, however, attempt to shed light on certain aspects of medical and public health entomology which have not been brought to light here, and to add some additional information to the topics discussed today especially the one pertaining to insect juvenile hormones and other growth regulating substances.

In discussing the relationship of pest control methodologies to the environment, investigators sometimes unknowingly or intentionally make generalizations. It is sometimes stated as all or none effect, depending as to who is drawing the conclusions. However, in a gathering of this type assembled here, I have not seen or come across such unqualified general statements or conclusions presented in the papers.

Dr. Provost in his presentation pointed out the complexity of environmental problems, the need of environmental quality for survival of biological systems. He emphasized that the aesthetic and cultural significance of the environment is related to the interpretation based on values, background and experiences of the community and society as a whole. Then he expertly discussed the deterioration of environmental quality due to various activities of mankind for the purpose of procuring food, shelter and pleasure.

In discussing the environmental aspects of biting fly control programs, Dr. Provost implied that residual house sprayings with DDT, will enhance rather than degrade the environmental quality. In suburban and rural areas, biting fly control is a necessity for good living and that conservationist and ecologist like the rest of us desire suppression of blood-sucking insects such as mosquitoes, *Leptoconops*, tabanids and others. In wilderness areas, source reduction such as drainage, impounding and other practices are either impractical or undesirable.

Dr. Provost alluded to the constant level of crop damage by insects despite the most modern technology of insect control. This statement, of course, has not taken into account the tremendous increase in monoculture of crops and the rapid transport system which aid in the dispersal and dissemination of injurious insects. Dr. Provost concluded by saying that biting fly problems can be solved to a great extent if we are given the resources and time to develop the necessary basic and applied information on the biology, ethology and impact of biting flies and the overall environmental interrelationships. This discussant fully agrees with this conclusion.

The paper presented by Dr. Hocking was full of deep thoughts and philosophical pronouncements. He implied that environmental quality should be protected at a level which is beneficial to man himself as well as animal and plant life. The highlight of his presentation was that pest control methodologies and environmental quality can be made compatible. The use of pesticides should be confined to emergency situations while scientists are engaged in developing comprehensive knowledge about the complex problems. He regretted that at this time as the problems of biting flies are getting out of hand and the solution to some of our environmental problems are greatly needed than ever before, the resources for attacking these problems are badly drying up.

This discussant fully agrees with Dr. Hocking's assertions and would like to point out the current distressed situation in job opportunities for new graduates in all fields of natural, and social sciences. We should all work toward the development of new programs in medical and public health entomology with a view toward solving some of the most pressing and widespread problems of biting flies which adversely affect human health and quality of living in wide areas of the North American continent. Those in higher positions should be urged to allocate sufficient resources to research programs which affect the health and well-being of every individual in the society.

Dr. Hocking presented some practical and economical measures of personal protection such as the use of protective clothing, oral administration of repellents and use of contact or skin repellents. These measures although practical for those who visit or stay temporarily in fly-infested areas, will not, according to this discussant's opinion, work in the tropics or elsewhere for people who live in fly infested areas for long periods.

Dr. Hocking ended on the note that integrated control provides the best opportunity and promise for biting fly abatement.

In the area of chemical control developments, Dr. West emphasized the lack of information on the establishment of tolerance thresholds for biting flies. In the absence of such standards it is difficult to attack the problem of biting fly population management. This discussant agreeing with Dr. West, feels that establishment of economic levels or thresholds for important human pests is not possible at this time. This discussant, however, after researching the problem of aquatic midges in residential and recreational lakes in California, has arrived at tolerance thresholds of 60-120 larvae/ft^2 in some lakes. These levels of infestation in the bottom mud lead to sufficient numbers of adult midges which become a problem to most of the inhabitants on the premises located on the shoreline.

Dr. West reported on the efficacy of strip aerial application for black flies and found this method to yield excellent control at a rate of 1/10 of the total coverage. Materials of choice for black fly larval control at the present time are: Abate, methoxychlor and chlorpyrifos. The former two having a better margin of safety to nontarget organisms. For adult control, methoxychlor, malathion, ronnel and propoxur are quite effective.

Highlight of this paper was that aerial applications of chemical materials for the control of blood-sucking flies has done little damage to the environment. This discussant, although concurring with Dr. West in this regard, feels that the total impact of such treatments has scarcely been studied. Much more work is needed to assess the ecological and environmental impact of such areawide control operations initiated against biting flies.

Environmental impact of pesticides is influenced by many factors such as: persistence, stability, specificity and biodegradability, as reported by Dr. Saha. He reported that DDD has been found in large quantities in Clear Lake, California, but only smaller quantities have been detected in the St. Lawrence. This could be due to the nature of the topography and use pattern of pesticides in an area. Clear Lake acts as a sink for a large area of tree fruit crops where DDT was used in large quantities. In the area most of DDT and its relatives are drained into the lake. Therefore, the bulk of DDE found in the lake could be attributed to agricultural pest control, rather than the control of *Chaoborus astictopus*, the Clear Lake gnat. Dr. Saha mentioned a very few cases, where biomagnification of organophosphate and organocarbamate insecticides has occurred. In research conducted by this discussant, parathion and Dursban (chlorpyrifos) have been found to magnify in mosquito fish (*Gambusia affinis*) and channel cat fish (*Ictalurus punctatus*), but the residues declined markedly in 3-4 weeks to insignificant levels.

The paper on the potential efficacy of insect juvenile hormones provided some new ideas and concepts regarding these materials. Dr. Strong, in his paper, reiterated that the molting hormone might attract more attention in the future. But the stigma attached to steroids might make the practical development of ecdysone rather difficult. Dr. Strong showed several JH-like compounds to have a very high level of activity in the range of 0.1 ppb or less in the laboratory. It should be pointed out that the dosages in the field may have to be increased 100 or 1,000 fold or suitable slow-release formulations developed which makes the hormone available over long periods of time.

Dr. Strong implied that the hormones are group specific; but in the view of this discussant, he is more or less considering acute toxicity. This discussant feels that little information is available concerning the chronic effects of JH on important components of the aquatic ecosystem. The speaker and this discussant feel that JH may provide another tool for the control of biting flies, but these should not be considered as a panacea.

As far as biting fly control is concerned, Dr. C. H. Schaefer (Univ. of California, Berkeley) working out of Fresno, and this discussant, working in Southern California, have studied a dozen or so JH analogues. Among these, two compounds have been found to manifest the greatest potency. Zoecon ZR-515 has been found to manifest high level of activity against *Aedes nigromaculis*, *Culex quinquefasciatus* and *C. tarsalis*. Another compound under development by Hoffman LaRoche Co. (RO-20-3600) also shows good activity against larvae of mosquitoes.

Some of the juvenile hormone mimics (insect growth regulants) act against a very specific stage of development of the 4th stage larvae. The larvae die just prior to completion of pupation or during the pupal stage. Other compounds seem to exhibit delayed effects even when 1st or 2nd stage larvae of mosquitoes are treated. Whether this is due to the stable nature of the compound or delayed effect carried over from the earlier instars is not known at this time.

Dr. Haufe's paper on systems evaluation presented some complex environmental interactions and pointed out the inadequacies of technical evaluation and assessment methodologies. He discussed the various parameters of population measurement and discussed the practicability of some available methods. He expressed the view that sequential sampling and development of information to lead to construction of life tables, are important procedures in assessing natural populations of biting flies.

Dr. McClelland presented some novel techniques to measure certain parameters of natural populations. The use of heavy metals can provide a good tool for marking insects for release and recapture. The heavy metals being stable, the marked insects recaptured can be stored indefinitely for future study and analysis.

From the contents of the papers presented on today's program, it appears to me that there is a tremendous lack of needed information which could provide a basis for the development and implementation of biting fly control programs. In the absence of needed and adequate research programs, the biting fly problem and environmental quality will suffer a great deal in the future. Time is of essence and a good start should be made as soon as possible.

OPEN DISCUSSION

Lefkovitch: I have a couple of comments, one which picks up an echo from the whole of today; the problem that we are facing here and elsewhere is one of conflicting demands. We want to minimize damage to the environment but at the same time to maximize human comfort; these two things seem to be in conflict. We want to get rid of some of our insects yet we don't want to affect our own and certain other populations. Now this is the classic problem that mathematicians face in optimality theory, for example, the minimax kind of idea. In this situation we are facing, it might pay off to formulate things exactly in this sense. What is it that we want when we say "minimize damage to environment"? We were talking about non-target organisms – do we want to minimize the damage there? Do we want to minimize the shift in whatever patterns of relationship exist between different species, the flow of energy through a system? You are much better at expressing this than I shall ever be, but this is the point that I want to make here.

The second point relates to Dr. Haufe's remarks and also to general systems models which are being discussed. Systems models, in my opinion, do not differ essentially from natural history. They are, in fact, what I think biologists do and have been doing from time immemorial. We look at what we find. We look at the relationships between this and that, different species or different life stages, what feeds on what and how many get eaten and at what rate, and so on. This is, in fact, a systems model. Now the difference between what is available today from the past, and there is a difference, is the degree to which such models can be used, constructed, amplified and manipulated; in this respect computers are an aid, but only an aid. There are other methods, but what is important, I think, and which can come across without computers, is the kind of logical thinking that computer science has led us into, both in mathematics and in life in general.

One of the things which computer science has made possible is extensive simulation. In Dr. Haufe's paper, the chart which he handed around contains a suggestion of a simulation model. I think, however, there is one aspect which is missing; it is that there is no feedback between the simulation model and how we might manipulate the environment. One of the objectives in simulating a system is to find what I shall call sensitive regions. There are some variables that we are prepared to feed into a system which may be relevant and which certainly in the laboratory can be shown to bring about a highly effective and immediate response. The question that a simulation model may answer in terms of this sensitivity analysis is "do these variables come into play in the natural environment"? Other variables may take over first. Fecundity may certainly be affected, for example, by density but in order to achieve that density there must have been a hell of a lot of larvae around, so many that these larvae would have completely eaten the food and subsequently starved to death, so that the population would never achieve that density of adults which would affect their fecundity. This is the sort of thing that sensitivity analysis in a simulation may show up. Those regions of a model which appear to have considerable effect, or a major effect, upon the competing maximizations and minimizations that we are trying to manipulate should be found: these may be the areas for research and for subsequent manipulation.

A few short remarks in connection with simulation are worth making. A model and its simulation seem to have become synonymous. They are, in a sense, but it's worth distinguishing between two kinds of models, the one which statisticians call parametric models, such as the analysis of variance, and simple-minded linear regression. These are attempts to summarize data to help their understanding without any pretence, this is the key thing, without any pretence to mimic the biological structure of the situation. It is most important not to read anything special into these sorts of model. They are very useful models; we have all used these techniques with some success, but they are not biological models. A simulation model can also be of a parametric nature, and can be quite informative. Now the other kind of model is what I call a deep model, it is one which in some sense tries to mimic the biological processes that we believe take place. Now these are much more difficult to handle, in the simulation sense, but they are certainly worth the effort.

Another distinction between models has been made today, namely between deterministic and stochastic models in the context of a distinction between biomathematics and biomathematicians. Many biomathematicians have certainly confined themselves to deterministic models and have found great difficulty in using stochastic ones; in consequence, some have not advocated their use. I would say that this is just a deficiency in biomathematicians not of biomathematics; there is an enormous amount of work available in this field which is perhaps a little bit elusive for the nonmathematician.

West: Those of you who heard me highly recommend Baygon as a blackfly adulticide should understand that the registration process is a long one. Registration is not easy to obtain these days. The material has to be evaluated in terms of the effectiveness claimed for it as an insecticide. It has to be acceptable to the food and drug people; it has to be acceptable to the fish and wildlife people and our wildlife people have okayed it. I am not aware of a high toxicity of Baygon to birds, I am not aware of it ever having been used for killing birds. I am aware that a quite different compound, the organophosphorous compound Baytex, is quite highly toxic to birds. It has been used for killing birds in Africa, I believe.

Fettes: In an earlier comment, Baygon was confused with Baytex and Baytex was said to be also known as Fenitrothion. All are very different materials and I think that this shows that one should be very very careful when naming compounds of any kind. Fenitrothion is being used over some eight million acres of forest this year and it is not a bird killer at the recommended application rates.

Frank. From what I heard Dr. Haufe say, there is no satisfactory method measuring a population before you start its control, so how do you measure it after treatment? How do you assess whether or not the treatment was effective?

West: The assessment of larval populations of blackflies is simplicity itself. As a standard sampling device, we use a lightweight plastic cone anchored in a stream. The larvae attach and can be counted. In our tests, for example, we had cones at one-quarter mile, one-half mile, three-quarters and one mile downstream. Counts are made just before treatment, an hour after treatment and 24 hours after treatment; one can calculate a percentage control figure. For adulticiding we do landing rate counts for blackflies just before and after treatment. These are not absolute figures, but if for example, you have counts of 50 insects landing per minute before and 5 per minute after treatment, the people that live and work in this area are quite willing to accept this as an indication of effective control. So I think we have excellent methods of indicating whether or not we get control with Methoxychlor as a larvicide, and it is an excellent larvicide, and with Baygon as an adulticide.

Hudson: I have a question for Dr. Strong. Did any of the hormone analogues he tried prolong the larval or pupal stages of the mosquitoes?

Strong: No, they did not. Normally speaking, when these compounds are applied at generally accepted levels, say a tenth of a part per million and down, they interfere in no way with the growth and development of the larvae. They do not interfere with pupation, they pupate normally, but they fail to emerge properly.

I have one other comment and that is that the slide that Dr. Mulla showed purporting to indicate the exceedingly low level of toxicity that you can obtain. I caution you to accept these with more than a large gram of salt. Occasionally, under very highly controlled conditions when you select your larvae very carefully and everything is exactly right, with ZR-515 you can get kills at this low level. But normally speaking, I think it is a mistake for you to go away from here with the idea that three-tenths of a part per billion will give control. I think that somewhere around a thousandth of a part per million is about as low as you can get with the better compounds and achieve control.

Smallman: We have heard a good deal today about the difficulty of determining whether a compound or a breakdown product is innocuous at some level in the ecological hierarchy, and with this in mind I would like to ask whether or not the juvenile hormone analogues have been studied for their possible effects on microcrustaceans and for that matter on bacteria? These would be very important effects on the ecology in general.

Strong: Yes, they have been to some extent, but I know of no published literature in this regard at all. I do know that as far as the microcrustaceans are concerned, I myself have tested for direct toxicity, not to see what prolonged effects would be observed, but for direct toxicity against copepods and other organisms normally found in fresh water aquatic systems. I found no direct toxicity going as high as a thousand parts per million. I cannot answer the question what would happen if we prolonged this.

Corbet: In the forthcoming field trials which you intend to conduct using juvenile hormones, how do you plan to assess the effects on non-target organisms?

Strong: We don't, and the reason that we do not is twofold. One, we do not have the manpower to do it. Secondly, most of our work will be in flooded areas (we are aiming our experiments specifically at mosquitoes) and I don't think we have the non-target organism problem that we have say in a rice field. If we do apply this material to rice fields or to permanent ponds then we must certainly look at non-target organisms.

Mulla: As Dr. Strong mentioned, it is extremely difficult to have these compounds evaluated against the target insects, let alone the non-target organisms. As far as acute toxicity is concerned, we don't see too much of a problem because this is not the mode of action of these types of compounds. You have to study the long-range effects, the effects on the ecosystem dynamics. For the past year and a half we have been working with one species of mayfly. In the first place, we had no idea how to sample this mayfly, and secondly, we didn't know how many aquatic stages or nymphal instars there were in this particular species. The treatments were made with the growth regulator ZR-515 in the range of one- to two-tenths part per million. These concentrations produced 95 to 100 per cent inhibition of emergence of asynchronous populations of both *Culex tarsalis* and two or three species of chironomid midges. The first few tests showed no toxic effects on the mayfly, but now we are finding that if you get the last nymphal instar of the mayfly and isolate this, it is affected in the same manner as mosquitoes and chironomids. In other words, they do not emerge normally from the pre-imaginal skin.

In the field we know that the minimum concentration that we need for 90 per cent effectiveness is in the range of 0.1 ppm and this, of course, is almost one hundred to one thousand times as much as the effective laboratory concentration.

Khan: I would like to know if some information is available on the toxicity of juvenile hormone analogues to vertebrates, particularly laboratory and farm animals?

Mulla: I don't believe any studies have been conducted on farm animals, but all the toxicity data so far accumulated are on rabbits, mice and guinea pigs. I think long-range feeding studies are in progress now to see if some of these compounds have any carcinogenic or other deleterious effects on animals.

Provost: I wonder if there might not be an advantage in a half-life of juvenile hormone analogues of two to five days, speaking for the environment. I think that you could probably use these chemicals very effectively against *Aedes* and some of our *Culex* in Florida. This action would soon be gone and your chances of getting non-target larval dipterans would be very small. But if you go to some chemical which is effective for an entire season, sooner or later you are liable to hit and kill just about the majority of aquatic dipterans, some of which may be beneficial.

Strong: If we can extend the life of the material to 35 days in the laboratory, hopefully we will be able to extend it to say six days in the field. We are a little bit short right now, two to three days in the field is about a day to a day and a half shorter than we would like for good control of *Aedes*. If we can get it for just another day or so longer so that we can pick up those that are in the early thirds and hold it in the field long enough for them to move into the fourth stage and become sensitive, they will get caught.

Service: I'd like to ask Dr. McClelland a question. He mentioned he had a recapture rate of his marked mosquitoes, I think he said of 12 or more per cent, and if I can remember correctly, this was on his work in Tanzania. I understand this was a recapture rate of mosquitoes marked and then recaptured at the same place. I was very interested in this because this is quite a high percentage recapture. In England we've been marking mosquitoes but not in quite the same fashion. We've been marking them as I call it 'on their birthday', the day they emerged from their aquatic habitats. We marked them, released them and then caught them back at bait and got a recapture rate of 8 or 10 per cent. Have you any idea as to why you get this rather large recapture rate? It would suggest to me that they disperse very little from the area in which you're marking them.

I would also like to know, is it possible to incorporate the trace elements in paints in marking mosquitoes?

McClelland: In answer to the first question, I realize that the recapture rate of 12½ per cent was high and I have attributed that to the particular habitat where we did the study, which was an old junked auto dump on the suburbs of Dar es Salaam with an enormous breeding population of *Aedes aegypti*. I have just assumed that this is a fairly closed population of about one acre and there was very little dispersion. I would have expected more dispersion in your *Aedes* population in England. Regarding the second question, I had thought about incorporating the trace elements in paint and certainly it would be much simpler to apply just a single dab of paint instead of having to worry about putting the spot in a particular place. I would say that if your daily anticipated capture rate was within the bounds of hand marking, that this would probably be much more preferable. A mark on the thorax with enamel paint would have a less adverse effect on the mosquito than the dust.

Corbet: First of all, Dr. Service made a remark in connection with the high recapture rate in Dr. McClelland's marking work. Without knowing of any detailed studies that demonstrate this, I would have expected from the synthesis that Johnson has carried out on migration and dispersal in insects, that if mosquitoes were marked on their birthday and recaptured later, the recapture rate would be very much lower than that which Dr. McClelland has described. In many insects the main dispersal phase comes soon after emergence and if mosquitoes were being caught at the beginning of a gonotrophic cycle it would seem likely to me that the main dispersal phase would already be over. Also I wanted to refer to this question of monitoring for effects on non-target organisms and I'd like to recall a discussion which the Advisory Committee on Entomological Research of the Defence Research Board had about a couple of years ago, as a matter of fact, I think it was at the same meeting that Dr. Hudson referred to when the suggestion of this Symposium originally came up, and at that time it was the Committee's feeling that monitoring for effects on non-target organisms, at least some non-target organisms, really ought to be part of the package when a pesticide is tested in the field.

SUMMARY

Rapporteurs . . . . J.J. Fettes and I.S. Lindsay

The President of the University of Alberta, Dr. Wyman, said something that should be taken seriously. He said that we have lost the initiative as scientists, and I think we have, entomologists in particular have lost the initiative. He said that we have to await a new cycle in science until we get away from this anti-education feeling. We should try to influence that new cycle in some way because we seem to be failing to convince anyone that what we are trying to say and do here is important. We know it is very important, but somehow we are not convincing those people who have the money nor those people who need the service.

We think Dr. Provost was trying to tell us that we must reconcile control with environmental quality and also that, in many situations, DDT was an enhancement of the environment. We need new methods for gathering more sophisticated knowledge of the total environment through research, and we have to find out some way of communicating with the layman. Dr. Provost ended by saying that it is the ethics of science and not the science of the environment that we are thinking of here and that we need doom-challengers rather than doom-sayers, and in this case the entomologists have got to be those challengers.

Dr. Hocking emphasized the need for the definition of a number of terms, particularly that of "environmental quality". He asked such questions as 'how clean? ' and 'for man and also for plants and animals? ' He emphasized the need for an improvement in communications between the scientists, developers and, of course, the public and the press. My own experience (I.S.L.) has been that this communication to these agencies from scientists in entomology is one that requires constant repetition. Dr. Hocking commented on "control versus eradication". In discussing some of the more important problems he outlined the history of the control of biting flies in Canada and some of the supporting organizations and committees that had been largely responsible for keeping this field coordinated, in an informal way, through the years. He emphasized the need for personal protection and of course the Department of National Defence agrees with this. It is one of DND's primary requirements, particularly now that there is increased emphasis on the Canadian North. Repellents are one of the prime essentials for individuals in the field. Military people are frequently required to operate away from large units or establishments, and protective clothing and biting fly repellents are almost their sole means of continuing to operate effectively. Dr. Hocking mentioned the need for clothing of sufficient thickness that the mosquito is not able to probe through it. Another point he mentioned was the possibility of using biting fly repellents on an area basis.

Dr. Hocking suggested the usefulness and the application of insecticides in the form of granules and he implied that there was a need for additional study and for some expansion of the application of this form of biting fly control. He then reviewed a number of additional subjects including the requirement for specificity of application techniques and ground application versus air spray. He felt that acceptable biological methods are a long way off and that we are going to have to look very carefully into the use of chemical control methods and into the possibility of integrating these methods with those of a biological nature.

In summarizing the paper of Dr. West, we have just one overriding comment, 'Baygon is great! ' Also, there is one little aside, Dr. West says that the control of biting flies has decreased through the years. Our comment is that there may be a decreased requirement for protection by people who work in air-conditioned offices, but not for those who work outside such insulated environments. He mentioned the use of particulate material of specific sizes for the control of black-fly larvae. This was a highlight in some of the work that he has done and it is research that he should be encouraged to continue.

Dr. Saha told us that we should look at not only the biological effects and the biological needs but that these should be coupled with more chemical knowledge and more physical knowledge of the compounds that we are using and how they affect the environment.

The paper by Dr. Strong included a very interesting historical review of juvenile hormone research. He said that the level of emergence of adult mosquitoes treated with juvenile hormone analogue is related to dosage. He also stated that some of the analogues have a very short half-life, particularly in non-sterile conditions. In outlining some of the problems he mentioned that the physical chemistry of these compounds is not yet clear and such problems as solubility and surface effects require emphasis. Sandy soil reactions appear to be reasonably good but not much is known about other types of soils. At present there is little knowledge of the effect of the analogues on non-target organisms.

Dr. Strong suggested that it may be possible to increase the half-life of some of the more promising analogues under field conditions. He admitted that it was possible that resistance to these compounds might develop. It was obvious, from the amount of discussion on the subject, that Dr. Strong and Dr. Mulla have simulated a great deal of interest in this particular technique in Canada.

Dr. Haufe's paper was one that surely interested all of us, but he probably scares some of you like he scares us. Biologists in general steer away from the real use of mathematical models as a systems approach to populations. Dr. Haufe pointed out the need for a real methodology in approaching definitions for the many sub-systems within the ecosystem to give ourselves a better idea of how to find the key factors and measure the effects and the interplay of integrated methods of control.

Dr. McClelland stated that one of the problems with field research on adult mosquitoes has been the lack of reliable field estimates, that is, estimates of the absolute parameters of natural populations. He described two new approaches to this problem, firstly, the selective sampling of a particular physiological phase and, secondly, the use of fluorescent dust together with trace elements for mass-marking with a large number of distinct codes.

Dr. Frank reviewed his own personal experiences with biting flies and suggested that Canada was perhaps fortunate to have a northern environment with large populations of biting flies, because these have probably protected it from man himself. He suggested that too often we begin field control applications before sufficient basic information has been obtained. He proposed that the integrated approach to biting fly control is the most logical one. He mentioned that DDT as a particulate was not favoured by his own organization, especially when it was used in deep cold water, and he presented some evidence on DDT residues. Dr. Frank was enthusiastic over the potential of juvenile hormone analogues. He distinguished between the need for urban, rural and wilderness control methods. He also emphasized that the wilderness problem should be based on personal protection rather than the application of chemicals or other field techniques.

Dr. Harris described some parallels in the control of agricultural insects and biting flies. He suggested that perhaps the main reliance would have to continue to be on chemical control. He also felt that current methods of personal protection would not be widely accepted by the civilian population. Dr. Harris suggested that DDT use in agriculture in Canada had been a serious factor in pollution, but he added that agencies concerned with the control of biting flies were also seriously involved. He criticized the switch from DDT to other compounds, many of which were not well understood, particularly from the residual point of view. He felt that much more fundamental work on residues and residue problems was required. Dr. Harris mentioned that some organophosphates break down into other toxicants and that the use of the term "innocuous" is not warranted. He stated that juvenile hormones are also chemicals, and these require concentrated study for their possible side effects. He mentioned the need to study the possibility of the development of resistance among juvenile hormone analogues. Included in his recommendations were the following: there is need for better control of pesticide use; legislation must be based on scientific data; we need improved methods and facilities for residue analysis; and, finally, we must develop integrated methods of control of biting flies.

Dr. Mulla made two general statements that should be highlighted. In his discussion he told us that our approaches to entomological problems are usually too general. We include too many generalities. Resources should be adequate for a complete study of environmental impact rather than permitting only piecemeal attempts. He also suggested that control decisions should involve those who live with the problems, and not be decisions made by those who do not understand, or have not experienced, the problems.

If we may be allowed to make one or two observations here on what has emerged from today's program, we have stressed over and over again our inability to convince governments of the importance of research in the entomological and pesticide fields. We have highlighted the lack of technological capacity and competence. We declare them to be below the requirement for the fields in which we are interested. One could list about ten or twelve specialities that should receive much more in the way of support. In many areas the funds are actually shrinking, rather than multiplying as they should as the problems increase in significance. We know from what we have heard today about ecological studies, that each one of them becomes vast. There is no longer a small problem, studies must include all organisms that are living in the places with which we are interfering, that is to say the total population, and therefore the resources input should be increased manyfold.

There is one more remark arising from the discussion. Dr. Lefkovitch said that we are trying to do two things that seem to be mutually exclusive, the manipulation of ecosystems for our own comfort while trying to maintain the environment unspoiled. We believe that the concern and the accent on the need for ecologically acceptable control methods which have emerged from this symposium suggest that these two things can be brought together.

BIOLOGICAL CONTROL AND ITS APPLICABILITY TO BITING FLIES

Ernest C. Bay
Department of Entomology
University of Maryland

Biological control has been an accepted entomological discipline since approximately 1888, or the time of the successful control of the cottony cushion scale by the vedalia beetle. There is a story about this success with which this gathering should be aware before we discuss the prospects for the biological control of biting flies. The story, as told by Mr. H. Compere, an emeritus at the University of California at Riverside, is that of the "ladybird fantasy and the great crusade" (Compere 1969). The vedalia beetle *Rodolia cardinalis* Muls. is a ladybird beetle that was imported from Australia in 1887 against the introduced cottony cushion scale *Icerya purchasi* Mask. This scale was about to destroy the citrus industry that was at that time the mainstay of the Southern California economy. This particular ladybird beetle proved to be an unqualified success, and within the two years after it was introduced it established a balance with the scale to where both species became difficult to find, and have since existed in a perpetual game of hide and seek. This is biological control at its best.

The fantasy of course ensued when, beguiled by this success, many California orchardists assumed that with further exploration and more ladybird beetles of different kinds, their other scale problems would be as easily solved. Such was not the case and many growers suffered seriously by abandoning chemical and other control measures while relying heavily on the hope of biological control as a panacea.

The fact of the vedalia success related to many factors. Both the cottony cushion scale and later the beetle were introduced from an area where the scale was not a pest. Unlike most ladybird beetles, that are relatively general feeders on homoptera, the vedalia is highly specific to the scale, and individuals must seek these out as if their survival depends upon it, for it does. Also, whereas most ladybird beetles require many prey on which to complete development the vedalia, being quite small in relation to its host, can complete its development on a single host specimen. In this and in other respects it behaves more like an insect parasite than like a predator. These and many other factors, combined as if in a formula, contributed to the success of this particular incident of biological control. A word of caution is appropriate here, that there are also predators which are not host-specific but, which as a part of other formulae are excellent biological control agents. Although the vedalia and the cottony cushion scale comprise the most celebrated case of biological control, there have since been many more that have approached, equalled or even excelled it as in the case of the control of the citrophillus mealybug (Compere 1932). Despite all that we know in analyzing these successes, however, we still cannot go afield and look for a preselected set of characteristics in a natural enemy and be assured that if introduced against a particular pest in a particular region it will prove successful.

During most of this time following the vedalia success, such efforts at biological control as have been made, with few exceptions, have been directed at strictly agricultural pests. Not until 1960, when serious concern began to develop for the limitations and side effects of chemical pesticides, did this approach for medically important insects begin to receive significant attention (A.I.B.S. 1960). In 1960 a symposium was convened by the American Institute of Biological Sciences in conjunction with various armed forces interests in Washington, D.C. to discuss the status and prospects for medically important insect control by biological means. In 1961, inspired by the interest which developed from this symposium, Dr. Charles Fleschner, then head of the Department of Biological Control at the University of California added a continuing program in his department for this research. Initial studies were directed at finding parasites and predators for the control of the non-biting *Hippelates* eye gnat, and mosquitoes in California. Other insects that have been concentrated upon in this laboratory since 1960 include chironomid midges, because of their nuisance significance, and various muscoid flies. Some of the findings of these projects will be discussed (Bay 1967, Bay and Legner 1963, Legner *et al.* 1966, 1968; Legner 1970). In recent years the Division of Biological Control in the Department of Entomology at Berkeley has developed a similar biological control program with efforts directed mostly at mosquitoes, but with projects also aimed at other medically important insects.

Within the last decade the World Health Organization has especially advanced research and documentation as to the importance of natural enemies in the control of biting flies and other medically important insects. Dr. Marshall Laird who is now Head of the Department of Biology, Memorial University of Newfoundland, actively spearheaded international research and cooperation in this area of biological control during the years that he headed WHO's former laboratory of Environmental Biology. The work now continues mostly in the WHO office of Vector Biology and Control. Among its activities WHO supports an International Reference Center for insect pathogens under the direction of Dr. John Briggs of Ohio State University where specimens can be sent for identification and rearing. It also supports a limited number of research grants, and sponsors pilot field studies of promising biological control agents in its various research units stationed about the world.

Before considering and assessing the advances that have been achieved in the biological control of medically important insects within and prior to the last decade, it is well to consider something of the facts and concepts of the discipline itself. There are seemingly good reasons why biological control was so long restricted to agricultural insect pests and weeds.

One important premise of biological control is that few insects very often achieve pest status in the presence of natural enemies with which they have evolved. Exceptions most commonly occur when man alters the environment through agriculture or other means to favor the pest insect over its natural enemies. Clear plowing and large scale monoculture, for instance, afford ideal conditions by which phytophagous insects can maximize their reproductive potential for at least one, and perhaps two generations, before leveling at destructive population densities. These high population thresholds are abetted by host crops that are uniformly planted and often genetically selected for uniform development, maturity and harvest. Natural enemies must rely on the host insect being already present before they can reproduce to effective numbers, which in the case of seasonal crop monoculture is often too late. In a natural ecosystem where plant development is relatively staggered and where alternative hosts occur, there is more opportunity for natural enemies to become effective and for pest-natural enemy populations to interact for a longer time at lower densities. Another upset of monoculture is that many insect natural enemies, especially hymenopterous parasites, require more than the host insect in order to thrive and reproduce. Other requirements include plant nectars, pollen, and protection from dust and desiccation that is often lacking in open, weed-free rows of evenly spaced plantings. Insecticides, too, are often more destructive to natural enemies than to target organisms. One of the arguments against the use of unselective pesticides is that by their destruction of natural enemies they sometimes elevate non-pest insects to pest status thereby substituting one or more new pests for the original key species. When it is understood that many agricultural pests are not adequately controlled by their natural enemies primarily because of man's interference, one can easily question the probability for further natural or biological control of medically important arthropods including ticks, chiggers, mosquitoes, tabanids, simuliids, stomoxys, rhagionids, culicoides, and others in those many situations where these are pests without man's assistance. Another important reason why medically important insects have historically been ignored as subjects for biological control is that most of these are either considered indigenous to the areas where they are a problem, or like the housefly, are thought to be so ubiquitous as problems that effective natural enemies simply do not occur. Earlier I mentioned as a premise of biological control that insects seldom become pests among those natural enemies with which they have evolved. Classical biological control has mostly relied, therefore, on foreign search and introduction of parasites and predators that keep introduced pest species from achieving pest status in their native lands. Most of the outstanding biological successes to date support this philosophy, although progress is being made and success is being achieved in other biological control technologies including periodic mass release of native parasites and predators, habitat management including the use of selective pesticides, and alternate host planting and strip harvesting to conserve natural enemies, establishment of field insectary plantings to promote early season natural enemy buildup, and sprayed food supplements to substitute for nectar and pollen in weed-free monoculture. Also encouraging and rewarding are developments in insect pathology. It is innovations and approaches such as these which encourage biological control attention for some, but not all medically important insects. There is at least one reference (Parman 1928) where egg masses of *Tabanus hyalinipennis* Hine parasitized by the parasite *Phanurus emersoni* Girault were mass collected and distributed in heavily tabanid infested areas along the Edwards Plateau in Texas with a reported 50% destruction of tabanid eggs during favorable seasons. Legner *et al.* (1966, 1968) have succeeded in materially improving housefly control on several southern California poultry ranches by manure management designed to conserve and increase the efficiency of coprophagous fauna, pupal parasites and predators. Periodic mass release of the top minnow *Gambusia affinis* Baird and Girard for mosquito control is a common and effective practice by mosquito abatement districts in California and neighboring states. Hoy and Reed (1971) recently found that as few as 100 gravid female *Gambusia* per acre, released in May in California rice fields, gave better than 81% *Culex tarsalis* control for the season.

Jenkins (1964) compiled an annotated bibliography of pathogens, parasites and predators of medically important arthropods and recorded more than 600 pathogens and parasites known to cause either mortality or morbidity, and more than 900 predators. Some of these including planarian flatworms and hydra offer enticing characteristics as agents for mosquito control but, except for fish (Bay 1967, Gerberich and Laird 1968) none have so far found practical application. Records for most of these organisms apply either to simple host-parasite observations, or to predatory capability of organisms confined to laboratory containers. In my own experience, while studying various predators of mosquitoes in pond habitats I have never found any that are regulatory in the sense of being specifically dependent upon mosquito larvae as prey. Most mosquito predators appear to be substitutive mortality factors in the sense described by Richards (1961). These compensate for one another, and for variations in physical mortality factors within the environment so that mosquito population equilibrium for a particular habitat remains relatively stable throughout succeeding generations. If an introduced natural enemy is to be effective in reducing this population equilibrium it must add a mortality factor and not merely substitute to further compensate for fluctuations in existing mortality factors.

Theoretically, we have at least one advantage in dealing with biting flies, compared to most commodity pests, in how late into the life cycle of a particular generation additive mortality factors can be employed. This is because among biting flies it is only the adult with which we are concerned whereas among commodity pests it is usually the immatures that are most injurious. Owing to the surplus of adults that are produced by many insects compared to their progeny that a given ecosystem will support, it is conceivable that adult populations can be reduced without affecting the status quo of succeeding generations of immatures. Some indication of this is had by the general control ineffectiveness of light traps and other mechanical devices, except where these have been used on a very concentrated basis to protect a limited crop or breeding area. Offsetting the theoretical advantage of leeway that I have just described in finding and introducing natural enemies of biting flies, is the more real factor of pest tolerance. The population reduction of any pest that constitutes control is at best an arbitrary matter, and this is especially true with biting flies. The determination becomes more critical when the biting fly is also a disease vector. In many situations a biting fly population may be the lowest that can be achieved by natural or biological methods and still be considered in need of control. Furthermore, as with commodity pests of agriculture, man often aggravates his problems with nuisance diptera by his own activities and alterations of the land. Mosquito problems may be enhanced by irrigation practices that favor *Aedes* mosquito populations and by organic pollution favorable to *Culex* species, while these practices disadvantage their natural enemies. Likewise, manure handling by frequent cleanout of poultry houses eliminates stabilizing populations of natural enemies (Legner and Olton 1968), and manure steeping provides a more convenient habitat for houseflies while protecting immatures from predation and parasitization to which they would be exposed in scattered droppings (Legner 1970). *Hippelates* eye gnats in the Coachella Valley of California are encouraged by agricultural practices that increase their food supply, oviposition sites, and protection from most natural enemies (Bay and Legner 1963, Bay unpublished research).

Further problems to be considered in seeking biological controls for biting flies include that some species, such as pool and container-breeding mosquitoes, breed in a variety of conditions in a particular location so that an effective agent in one type of breeding site might not succeed in another and might not visibly affect the adult population as a whole. Agricultural commodity pests, by comparison, are usually more restricted in their breeding sites. Furthermore, agroecosystems besides aggravating many pest problems by favoring the pest insect are also more well defined, more accessible, and therefore more amenable to management in redressing conditions that have created the problem than are many natural ecosystems producing biting flies and other arthropods of nuisance and medical importance.

Although I have here pointed out some of the difficulties we must face in finding and employing natural enemies of medically important insects compared with pests of agricultural commodities I feel that this is a viable area that we must continue to pursue. No single enemy of any given pest that we might find is likely to have the impact, efficiency and convenience of the pesticides to which we have become accustomed. Insect pathogens appear to have the only potential for approaching comparison. Guided by this understanding our effort should be to avoid environmental modifications that interfere with existing natural enemies, and to look for ways of encouraging or releasing agents that we have reason to believe may have additive mortality capability in those breeding sites where they should, but do not, exist.

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*Fig. 1. Two planarian worms (*Dugesia *sp.) coil about a captured mosquito larva. Although planaria seem unlikely predators of mosquito larvae they can be effective mortality factors when confined with mosquito larvae in small, shallow water accumulations such as hoof prints of cattle, and receding puddles.*

Fig. 2. *A* Culex *mosquito larva carcass from which a planaria has devoured all musculature, leaving only the exoskeleton and gut contents.*

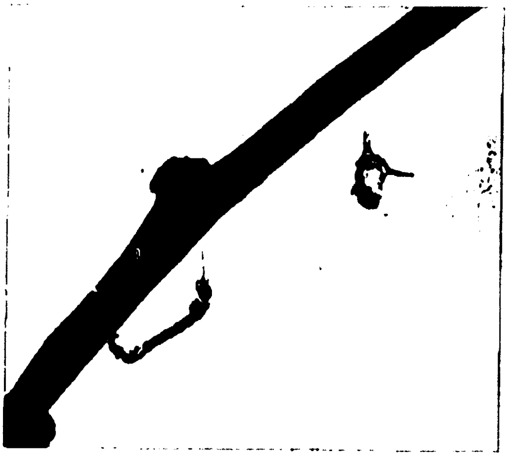

Fig. 3. Hydra americana *Hyman engulfing captured mosquito larvae. Hydra have been shown to be very effective predators of mosquito larvae in laboratory containers, and in limited field habitats. Studies are in progress at the University of California, Riverside and Irvine, to determine the feasibility of rearing and spraying hydra into suitable habitats for selected mosquito control.*

ASSESSMENT OF THE POTENTIAL OF SOME PATHOGENS AND PARASITES OF BITING FLIES

H. C. Chapman

Agricultural Research Service
U.S. Department of Agriculture
Lake Charles, Louisiana 70601

Although some pathogens and parasites of biting flies have been known for more than 100 years, only about 5 of the more than 150 known agents (Microsporida (protozoa), *Coelomomyces* (fungi), viruses, and nematodes) reported from biting flies [Ceratopogonidae (biting midges), Tabanidae (horse and deer flies), Simuliidae (blackflies) and Culicidae (mosquitoes)] have had even limited field releases (all in mosquitoes). This paucity of field releases indicates that few of these possible biological control agents have been mastered to the point that they can be disseminated.

As Table 1 shows, there are about 370 species of biting flies in Canada, but only a relatively small number have been reported as hosts of pathogens and parasites in Canada. I summarize here the potential of the most important species of pathogens and parasites as biological control agents against these biting flies.

TABLE 1

Species of Culicidae, Ceratopogonidae, Tabanidae, and Simuliidae found in Canada that are reported hosts of pathogens and parasites (Canadian records in parentheses)

Genera and number of species in Canada		No. found to harbor indicated pathogen			
		Microsporida	Viruses	Fungi	Nematodes
Culicidae					
Anopheles	6	3	1	4	2
Aedes	43	16 (1)	6	5	13 (7)
Culex	5	5	3	4	4
Culiseta	6	3	1	3 (1)	2
Mansonia	1	1	0	0	0
Psorophora	2	0	0	1	1
Uranotaenia	1	1	0	1	1
Wyeomyia	1	0	0	0	0
Ceratopogonidae					
Culicoides	50	3	1	0	5
Tabanidae	135	1	0	0	7 (3)
Simuliidae	120	22 (8)	0	1 (1)	16 (6)

Protozoa (Principally Microsporida)

Ceratopogonids. The only report of microsporidans in ceratopogonids found in Canada (*Culicoides* spp.) was that of Chapman *et al.* (1968) who observed *Pleistophora* spp. infecting an unnamed *Culicoides* larva from a pool and larvae of *Culicoides nanus* from treeholes. However, at my laboratory, we have found a new species of *Nosema* in larvae of the same species from another treehole. Nothing is known of the host-parasite relationships or the method of transmission of these diseases. Also, all attempts to transmit these diseases to mosquitoes were unsuccessful. The levels of infection observed in the field populations were always less than 1%

Tabanids. The only report of a microsporidan in the tabanids found in Canada was made by Gingrich (1965) who described a new species (*Thelohania tabani*) from larvae of *Tabanus atratus* collected in Mississippi. About 22% of the field population was infected, and the disease could be transmitted *per os* to healthy tabanid larvae.

Simuliids. Jamnback (1970) reported 15 species of Microsporida of the genera *Caudospora, Weiseria, Pleistophora, Thelohania, Nosema,* and *Octosporea* parasitizing blackflies. Of the 22 host species of *Gymnopais, Prosimulium, Cnephia,* and *Simulium* found in Canada, only 8 of the records were made in Canada. The levels of infection sometimes were reported to about 50%, but most ranged from 5 to 10% (Jenkins 1964). Also, the high levels may have resulted because larval samples were taken after the start of pupation. The methods of transmission of these microsporidans are relatively unknown, probably because of past difficulties in maintaining colonies of blackflies.

Culicids. Almost half the species of Culicidae reported from Canada have been reported as hosts of Microsporida by investigators in the United States; the single Canadian record by Welch (1960a) reported a *Thelohania,* probably *opacita,* in larvae of *Aedes communis.* The literature thus abounds in discussions of such subjects as hosts, host-parasite relationships, taxonomy, and transovarian transmission, but only 3 species of microsporidans (*Nosema stegomyiae, Pleistophora culicis,* and a *Stempellia* sp.) can be maintained with any regularity by *per os* transmission in the laboratory. All others (especially *Thelohania*) cannot be transmitted *per os* in the laboratory so the studies that are a prerequisite to eventual field releases cannot be done.

Pleistophora culicis was released on Nauru Island and infected some mosquito populations, but the results are inconclusive to date (Laird 1971). *Nosema stegomyiae* has appeared promising against many anophelines in the laboratory and has decimated or eliminated a number of colonies (Hazard 1970). *Stempellia* sp. is known only from *Culex p. quinquefasciatus,* and the levels of transmission in the field and laboratory are quite variable, often less than 10%; however this agent has been cross transmitted to several species of *Culex.*

Fungi (Principally *Coelomomyces*)

No important reports are known for fungal pathogens in either ceratopogonids or tabanids.

Simuliids. A single unconfirmed record exists of *Coelomomyces* in blackflies (from Central America). Also, *Coelomomycidium* is known from blackflies and has been found in larval populations in Newfoundland.

Culicids. Almost a third of the 62 species of mosquitoes found in Canada have been reported as hosts of *Coelomomyces* in the United States, but the only Canadian record of this fungus is that of Shemanchuk (1959) who reported that 12% of all larvae of *Culiseta inornata* collected in southern Alberta were infected with *Coelomomyces* near *psorophorae.* In the field collections made by my laboratory, the highest reported levels of infection of *Coelomomyces* spp. in mosquito larvae were as follows: 95% in *Culiseta inornata* and *Psorophora howardii*; 97% in *Aedes triseriatus*; 85% in *Culex peccator*, and 94% in *Anopheles crucians.* Also Muspratt (1963) reported levels as high as 100% in populations of *Anopheles gambiae* in Zambia.

Coelomomyces has persisted in some Louisiana ponds for at least 6 years and has reoccurred after prolonged periods of drought (29 weeks). In addition when Laird (1967) released a *Coelomomyces* on a Pacific island, the fungus established itself in local populations of *Aedes polynesiensis,* a common vector of filariasis.

Several species of fungus have been maintained via *per os* transmission in the laboratory (Couch 1967;

Madelin 1966), but the mode of infection, answers to questions of host specificity, and a satisfactory method of germination of resistant sporangia still elude most investigators.

Viruses

Ceratopogonids. The only record of a virus in biting midges (an iridescent virus (CUIV)) was that of Chapman *et al.* (1968) in larvae of the treehole breeding *Culicoides arboricola*; almost 50% of the larvae collected from a treehole over 11 months were infected. However, larvae infected with the virus have been found in only 3 treeholes. When infected cadavers were released into several treeholes, only one such habitat eventually produced some infected larvae.

Tabanids. Viruses are not known from deer and horse flies.

Simuliids. The sole report of a virus in blackflies was that of Weiser (1968) who found a larva of *Simulium ornatum* in Czechoslovakia infected with an iridescent virus (SMIV). No transmission was attempted because the specimen was used for electron microscope studies.

Culicids. the first virus reported from mosquitoes was a cytoplasmic polyhedrosis virus (CPV) that infected the leg, wing, and antennal buds of larvae of *Culex tarsalis* in California (Kellen et al. 1963, 1966). However, this same probable virus was reported from larvae of *Culex salinarius* in Louisiana (Clark and Chapman 1969), who also noted similar tetragonal crystals in a larva of *Anopheles crucians*. Transmission of this CPV is difficult, and the level of the disease in natural populations is always low.

Mosquito iridescent viruses (MIV) were first reported from larvae of *Aedes taeniorhynchus* in Florida (Clark *et al.* 1965) and from larvae of *Aedes cantans* and *A. annulipes* in Czechoslovakia (Weiser 1965). Additional hosts of MIV are now known to be *Aedes detritus* (Tunisia), *A. dorsalis* (Nevada), *A. fulvus pallens* (Louisiana), *A. sticticus* (Louisiana), *A. stimulans* (New Jersey and Connecticut), and *A. vexans*, *Psorophora ferox*, *P. horrida*, *P. varipes*, and *P. confinnis* all from Louisiana. Although levels of infection in the field have always been less than 1%, transovarian transmission is not uncommon and is thought to be the reason for survival of the pathogen in nature. The MIV remained infective in eggs of *Psorophora ferox* for at least 6 months in the laboratory, and the R-MIV was maintained through 68 serial passages in the laboratory in *Aedes taeniorhynchus* (average level of infection was 16%). Levels of infection were always much lower when the MIV was cross transmitted to other hosts of MIV. Attempts to infect larvae of various species of *Culex*, *Culiseta*, and *Anopheles* were always unsuccessful (Woodard and Chapman 1968).

Chilo iridescent virus (CIV), originally described from a pyralid moth, was readily transmitted in the laboratory to larvae of *Anopheles*, *Aedes*, *Culex*, *Culiseta*, and *Psorophora* though levels of infection seldom exceeded 3% (Fukuda 1971). Also the *Sericesthis* iridescent virus (SIV) isolated from a beetle was passed to larvae of *Aedes aegypti* (Day and Mercer 1964).

Clark *et al.* (1969) reported 2 occluded viruses from Louisiana, a nuclear polyhedrosis virus (NPV) in larvae of *Aedes sollicitans* and a CPV in larvae of *Culex salinarius*. Both infect gut and caecal cells, but the NPV is normally lethal, and the CPV is seldom lethal. Subsequently, similar infections of NPV have been noted in larvae of *Aedes triseriatus*, *Psorophora confinnis*, *Culex p. quinquefasciatus*, and *Culex salinarius* in Louisiana and of CPV in larvae of 16 species in the genera *Aedes*, *Anopheles*, *Culiseta* and *Psorophora*.

In the laboratory, NPV in *Aedes sollicitans* seldom exceeds 20%, but the virus has been transmitted to larvae of 5 other species of *Aedes* and *Psorophora*. Also, one field epizootic of the NPV-CPV (principally the former) infected a maximum of 71% of a larval population of *Aedes sollicitans* in Louisiana (Clark and Fukuda 1971), and two other epizootics of NPV in *Aedes sollicitans* in another salt marsh in Louisiana produced infection levels of 65 and 61%. This NPV can be disseminated into a habitat possessing early instar larvae, and the larval population will develop infections, however, if the habitat then dries the viral particles are apparently unavailable to the succeeding larval populations.

Nematodes

Ceratopogonids. Mermithid nematodes have been reported from biting midges since 1914. Smith and

Perry (1967) recently summarized the available literature and also reported that the emerging adult population of 3 species of soil-dwelling *Culicoides* in Florida commonly contained male intersexes caused by a nematode (probably a *Mermis*), that both sexes of hosts were parasitized, and that levels of parasitism ranged from 30 to 90% during the year. The nema in question has not been identified or cultured and it is not known which stage of the biting midge was parasitized initially.

In addition, two nematodes were reported as parasites of larvae of 2 species of biting midges in treeholes in Louisiana, a *Romanomermis* sp. in larvae of *C. nanus* and a tetradonematid nema in larvae of *C. arboricola* (Chapman et al. 1969); this latter species which was described as new (*Aproctonema chapmani*) by Nickle (1969), has not been seen in habitats since 1968. Parasitism by these 2 rather uncommon parasites is achieved by the penetration of the preparasitic stages into host larvae. Both species lend themselves readily to the culture technique used with some mosquito nemas (Petersen *et al.* 1968) and therefore could be maintained in the laboratory.

Tabanids. Four reports of mermithid nemas in adult *Chrysops* and *Tabanus* (one from Canada) and 2 reports of unidentified nemas in tabanid larvae were listed by Jenkins (1964). Also, Shamsuddin (1966) in a most interesting paper, reported parasitism (16-37%) of larvae of *Chrysops furcata* by a *Bathymermis* in Alberta, and this nema also infected as much as 70% of the larvae of *C. mitis* maintained on the infected soil. Penetration of the preparasitics into host larvae was observed, but no adult nemas were obtained nor was the nema cultured in the laboratory.

Simuliids. Mermithid nemas were first reported from blackflies in 1848. Our knowledge about the parasites was summarized by Phelps and De Foliart (1964). At least 16 species that occur in Canada (*Prosimulium, Simulium, Cnephia, Eusimulium* and *Gymnopais*) have been reported as hosts of nemas (*Gastromermis, Isomermis,* and *Mesomermis*), and almost half these records are from Canada. Nemas thus have been known in blackflies for almost 125 years, but the method of entry by the preparasitic into the host larvae is still not precisely known though it is suspected to be by ingestion. If that is true, it is quite unlike the penetration of hosts by preparasitics that has been observed in mosquitoes, chironomids, ceratopogonids, tabanids, and chaoborids. Also, the nemas may emerge from larval, pupal, or adult blackflies, and this emergence from the adult stage is thought to be the reason for the persistence of the nema from year to year in a specific stream. Some infections have been achieved in the laboratory, but none of the nemas has been cultured.

The cited literature mentions levels of infection in simuliid hosts that approached 100%, and in several instances, it was suggested that the nemas might have been responsible for the eradication or elimination of certain blackflies from habitats.

Culicids. Slightly more than a third of the species of mosquitoes that occur in Canada have been reported as hosts of mermithid nematodes, with at least 7 records (all *Aedes*) from Canada. Nemas were first reported in mosquitoes in North America in 1903 and probably about 35 species are now known hosts of about 8-10 species of nemas in North America.

In Louisiana mermithid nemas have at least 2 basic life cycles. In one, the preparasitic invades the host larva but grows very little and is passed through the pupa into the adult. In the adult, the nema grows rapidly, especially after the host female obtains a blood meal; emergence of the post-parasitic nema normally kills the adult mosquito. Nemas of this type (*Perutilimermis culicis* in *Aedes sollicitans; Agamomermis* sp. in *Aedes vexans* in Canada; *Agamomermis* sp. in *Aedes stimulans* in Michigan) are specific to one host. In the other type of life cycle, the preparasitic penetrates the host larva, grows rapidly, and emerges from and kills the host larva just before it pupates. Nemas of this type include *Reesimermis nielseni* and *Diximermis peterseni.* The former has a wide host range (22 species in the field and another 33 species in the laboratory); the latter is restricted to anophelines.

High levels of infection of mermithids in field populations of mosquitoes have been noted by many investigators (Jenkins 1964; Welch 1960b; Petersen *et al.* 1968). However, these researchers also mentioned that parasitism was generally restricted to a few habitats and that it was often absent in adjacent sites.

Mermithid nemas of multivoltine mosquitoes are easily cultured in the laboratory; for example, cultures of *Reesimermis nielseni* in *Culex pipiens quinquefasciatus, Diximermis peterseni* (= *Gastromermis* sp.) in *Anopheles quadrimaculatus,* and

Perutilimermis (= *Agamomermis*) *culicis* in *Aedes sollicitans* have been successfully maintained at Lake Charles, and methods of mass culturing were developed by Petersen and Willis (1972a) for *Reesimermis nielseni*. They also indicated that the inoculum produced by rearing and infecting five million larvae of the southern house mosquito each week in the laboratory could treat about 600 acres of mosquito breeding areas.

The first attempted release of a nema (*Romanomermis* sp. from a Zambian treehole) was made on Nauru Island; the results to date are unreported (Laird 1971). Also, Petersen and Willis (1972b) treated a number of field sites (ponds and ditches) in Louisiana with *Reesimermis nielseni* (mostly with a pressurized spray can) in 1971 and observed an average immediate parasitism (inundative effect) of about 60% in anopheline larvae. When the site was sampled just prior to the termination of nema activity due to low temperatures, the nema had recycled in many of the treated areas and parasitism approaching 47% was reported in one site. Recent data (1972) indicate that the nema has resumed its activity and appears to be established in most of these treated habitats. The extent of the inoculative effect of the nema on succeeding mosquito populations will be apparent after the sampling done this year.

Potential of Pathogens and Parasites

Microsporidans are therefore the most numerous and widespread of the pathogens in blackflies and mosquitoes, but most species cannot be used for control until they are readily transmissable in the laboratory. *Nosema stegomyiae* thus seems to have the most potential, especially against some of our malarial vectors such as *Anopheles albimanus*. Even so, the yield of this pathogen in *in vivo* systems is limited, and an *in vitro* system is needed for mass production of it or other likely microsporidan pathogens.

In the light of present knowledge, the greatest potential of a fungus appears to be that of *Coelomomyces* in mosquitoes. Some species of *Coelomomyces* are very persistent in nature and crop varying amounts of mosquito populations, but general field releases must wait until it is possible to produce large amounts of inocula in the laboratory.

Of the presently known viruses, NPV of mosquitoes seems to have the most potential, but research in this area is still in its infancy, and only time will show the real potential of viruses.

Nemas have a great potential as controls for many species of blackflies and mosquitoes, and might be promising for control of ceratopogonids and tabanids if the species that attack these biting flies were cultured. However, the use of nemas against blackflies must await the development of *in vivo* or *in vitro* techniques of culture. The latter technique would be preferable but would also be the most difficult. Indeed, even the development of an *in vivo* culture of such a mermithid nema means that a colony of simuliids would have to be maintained, the method of infection (penetration or ingestion) resolved, and techniques designed to recover and culture the nemas. The nema *Reesimermis nielseni* thus is the most promising of the nematodes because almost 6 years of intensive study have produced methods of mass culturing and release in the field against mosquitoes. Other such nemas undoubtedly can be brought to this point. However mass culturing nemas that have life cycles tied in with univoltine mosquitoes could present many additional problems which should be investigated by studying *R. nielseni* in univoltine *Aedes* since this nema from Louisiana (if it is the same species) was described from univoltine *Aedes* in Wyoming. Also, the potential of the nemas that infect adult *Aedes* such as *A. vexans* in British Columbia and *A. sollicitans* in the U.S. should be studied, and culture methods should be refined. Since this type of nema is distributed by adult mosquitoes, an excellent place to study such as the spread and rate of parasitism, might be an isolated coal mining area in the midwest with *Perutilimermis culicis* in *Aedes sollicitans*.

Obviously, only a few of the pathogens and parasites that might be used as biological control agents against biting flies have been studied sufficiently so that we can even determine their potential. Unfortunately, this field of study is years behind the successful work done with crop and forest pests. The lack of money and manpower and of direct and continuous assaults on the problem areas are probably responsible for this neglect.

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GENETIC CONTROL OF BITING FLIES: PROGRESS AND PROSPECTS[1]

K. S. Rai

Department of Biology
University of Notre Dame
Notre Dame, Indiana, U.S.A.

It was through work done with the venerable *Drosophila melanogaster*, an insect species and not too unoften a pest at that, that the science of genetics took shape during the early part of the twentieth century. Whereas genetic principles developed through work with this and several other species have been extensively applied for more than half a century now to improve cultivated plants and domesticated animals and to optimize germ plasm resources in all sorts of ways including the realization of the so called "Green Revolution", it is indeed most "surprising and rather disappointing" that the same principles "have not found greater application in pest management and control" (National Academy of Sciences, 1969).

The contention that insect control is in a crisis can hardly be debated. The traditional methods of control – use of synthetic organic insecticides – have in most cases proved ineffective and undesirable because of (a) the relatively rapid development of resistance on the part of insects treated, (b) their effects on the non-target populations, and (c) the massive environmental pollution that ensues from the use of such chemicals. The end results have often been verdicts such as "Moths 65 – USDA O", referring to USDA's "65-year, $100 million struggle against its lepidopteran adversary", the gypsy moth *Porthetria dispar* (Science 174:41, 1971).

Thus the history of organized struggle between man and insect pests makes it imperative that alternative types of control methods be developed and field tested. Although, various types of biological control methods have been suggested and attempted for more than 80 years (Clausen 1956, Turnbull and Chant 1961, Wilson 1965, 1970), difficulties of chemical control have brought about a renewed resurgence of interest in this area (Wilson 1971). In particular, genetic control which has received considerable attention during the last few years might provide one of the most desirable and powerful types of biological control. In simplest terms, genetic control involves any hereditary manipulation to suppress populations. Consequently, genetic methods which are often termed "autocidal" are of necessity based on utilization of individuals of a particular species to control populations of *that* species. Thus, *nothing alien* is introduced into the ecological niche of a pest population. Hence, maintenance of the environment in the original untreated form may be assured.

Unfortunately, appreciation of the role of genetics in applied entomology is in most cases no more than 10-15 years old. As a result, most progress in this area to date has been theoretical. Nevertheless, several developments during the last few years are indicative of a promising future for genetic manipulation of insect populations. Results obtained from some field trials with mosquitoes are particularly encouraging.

Understandably, mechanisms for genetic control for any species can emerge from a thorough investigation of the genetic biology of that species. Since any aspect of genetic analysis can be based only on

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controlled crosses, laboratory colonization of a candidate species becomes the first prerequisite for any and all genetic studies. Unfortunately, among biting flies, the simuliids and tabanids do not fulfill even this first prerequisite. As a result, relatively little is known about the genetic systems operative in these groups and any discussion of their genetic control, therefore, is definitely premature.

The story with mosquitoes is fortunately different, although here too, relatively little is known about the genetics of any Canadian species. This paper reviews the progress and prospects of genetic control in mosquitoes, although some examples from other pest species are also included.

Principles of Genetic Manipulation for Population Control

The basic principles and theoretical consideration underlying genetic control of insects have been adequately emphasized by Craig (1963), Knipling *et al.* (1968), Rai (1969a) and others and will therefore not be repeated here. In general, because of the propagation of the lethality or the sterility factors from one generation to the next and because of their emphasis on birth rather than death control, such methods should turn out to be much more effective and efficient than insecticidal or a good many biological methods. Ideally, eradication or replacement of a population following a single release of a desired genotype would definitely be most desirable; although in practice such a situation may be difficult to obtain. However, for species with relatively low reproductive potential, e.g. in the case of tsetse flies, such a possibility has indeed been suggested (Curtis 1968) and might well come to pass. One of the important features of genetic control is the specificity of a particular method to a particular species. Furthermore, it will be extremely unlikely that native populations will develop "resistance" in the traditional sense under pressure of control by the given genetic method.

Mechanisms Proposed for Genetic Control

Several potentially useful mechanisms have been suggested for genetic control of mosquitoes. Some of the more promising of these include:

a: Sterility

1. Mutagen-induced dominant lethality (Sterile-male technique)
2. Hybrid sterility (*Anopheles gambiae, Aedes mariae*)
3. Genetic-resulting from chromosomal re-arrangements: e.g. translocations (*Ae. aegypti, C. pipiens, An. Stephensi* and many others)
4. Hormone-induced (Matrone: *Aedes aegypti*)

b: Cytoplasmic incompatibility (*Culex pipiens, Aedes scutellaris*)

c: Competitive exclusion or population replacement – vectors by non-vectors (or pests by non-pests)

d: Conditional lethals; e.g. nutritional, temperature sensitive or non-diapausing mutants or recessive lethal mutation

e: Meiotic drive or sex-ratio distortion (*A. aegypti*)

Field Trials Involving Selected Mechanisms

Table 1 lists various field trials that have been undertaken with various species of mosquitoes during the last ten years in order to evaluate the feasibility of various methods of genetic control. The mechanisms that have been evaluated to date are:

a: Sterile-male technique

This technique is based on the induction of sexual sterility in males through the use of radiation or chemical sterilants and on inundating natural populations with such males (Knipling 1959). To a considerable degree, interest in methods of genetic control of insects is a byproduct of the successful application of the sterile male technique to control the screw-worm fly, *Cochliomyia hominivorax*, from southeast and southwest United States and the West Indian island of Curacao in mid-1950's (Knipling 1959). Curtis (1971) has reviewed the theoretical basis and some recent developments concerning induced sterility in insects. Although the sterile-male technique cannot be technically regarded as a type of genetic control because complete sterility cannot be inherited (NAS, 1969 and Rai *et al.* 1972), it is customary to treat it under genetic methods. Of course, the dominant lethal mutations that are induced in sperm of irradiated or chemically sterilized males and which result in male sterility are by

TABLE 1

Field trials for genetic control of mosquitoes

Species	Mechanism	Location & Agency	Reference
Unsuccessful or inconclusive:			
Aedes aegypti	Sterile male[a]	Florida, USPHS	Morlan *et al.* 1962
An. quadrimaculatus	Sterile male[a]	Florida, USDA	Weidhaas *et al.* 1962
Culex p. fatigans	Sterile male[a]	India, Govt.	Krishnamurthy *et al.* 1962
Culex tarsalis	Chemosterilant	California, DPH	Lewallen *et al.* 1965
Anopheles gambiae	Hybrid male sterility	Upper Volta, W.H.O. & ORSTOM	Davidson *et al.* 1970
Aedes polynesiensis	Competitive exclusion	Pacific, USPHS	Rozeboom & Rosen 1970 (unpublished)
Successful or current:			
Culex p. fatigans	Cytoplasmic incompatibility	Burma, W.H.O.	Laven 1967[b]
Culex p. fatigans	Sterile male[b]	Florida, USDA	Patterson *et al.* 1970
Culex p. fatigans	Sterile male[a,b,c]	India, W.H.O. & ICMR	Patterson, Sharma (unpublished)
Culex p. fatigans	Translocation	France, EIDLM	Laven *et al.* 1971
Aedes aegypti	Translocation[c]	India, W.H.O. & ICMR	Rai *et al.* 1972

a: Radiation-induced male sterility
b: Chemosterilant-induced male sterility
c: Trials continuing

definition drastic chromosomal aberrations and hence genetic in nature (Rai 1964). Nevertheless, they are not transmitted to the progeny.

The application of this technique for mosquitoes has been reviewed by Rai (1966, 1969b). In early sixties, this technique was tried with *Aedes aegypti* (Morlan *et al.* 1962), *Anopheles quadrimaculatus* (Weidhaas *et al.* 1962) and *Culex fatigans* (Krishnamurthy *et al.* 1962). All these trials were based on releases of males sterilized with radiation. The feasibility of a direct chemosterilant application to suppress an isolated desert population of *Culex tarsalis* was investigated by Lewallen *et al.* (1965). Unfortunately, measured in terms of reductions of the target populations, none of these trials were successful. The possible reasons for these failures are fairly well understood (see Rai 1969b). In general, they resulted either from the use of massive doses of radiation used to sterilize males as in the case of *A. aegypti* (Weidhaas and Schmidt 1963) or to releases of males with reduced fitness ensuing from a long history of laboratory colonization (Knipling 1959) as in *An. quadrimaculatus*.

More recently, Patterson *et al.* (1970) have been successful in applying this method to control a population of *Culex p. quinquefasciatus* from Sea-Horse Key, a small island off the coast of Florida, following daily releases of chemosterilized males during a ten week period. In work currently underway at the World Health Organization Research Unit on Genetic Control of Mosquitoes in New Delhi, India, Patterson, Sharma and coworkers are attempting to expand this technique to several villages in the vicinity of Delhi. Work with *A. aegypti* is also planned.

b: Hybrid sterility

When any two of the five sibling species in the *Anopheles gambiae* complex are crossed, the male progeny are sterile (Davidson 1964). Davidson *et al.* (1970) conducted a preliminary field trial to control a native population of *A. gambiae* species A near Bobo Dioulasso, Upper Volta, using such interspecific male sterility. The hybrid males released were produced by crossing females of an *A. melas* population from Liberia and males of a population of *A. gambiae* species B from Nigeria. They released approximately

300,000 hybrid pupae over a two month period at the end of the rainy season in 1968 against a naturally declining population of species A. The results of this field trial were negative although 75% of the males captured in the study village were sterile. Davidson *et al.* concluded from their results "that the sterile males were not mating on any significant scale with the natural species A females". Although several factors doubtlessly contributed to the lack of success in this field trial, a major flaw may be traced to the protocol itself whereby hybrid males produced by crossing two different species were utilized to compete with and control a third species. It would have been indeed surprising if the mating and behavioral differences among the males released and females of the native population would not have come into play, particularly under field conditions.

Coluzzi and Sabatini (1968) have demonstrated the existence of similar isolating mechanisms causing male sterility among Mediterranean populations of *Aedes mariae*.

c: Cytoplasmic incompatibility

The existence of incompatibility between certain allopatric populations of *Culex pipiens* is well known (Laven 1967a). Such incompatibility, which may be either unilateral or bilateral, and is maternally transmitted ensues from the death of the sperm nucleus in an incompatible egg cytoplasm before karyogamy occurs. As a result, no progeny are produced from such incompatible crosses.

This method was field tested with successful results in a small isolated village, Okpo, near Rangoon, Burma, under the auspices of the World Health Organization during an approximately 3-month period and five to six generations (Laven 1967b). The released incompatible male strain contained cytoplasm from a strain from Paris and the genome from Fresno, California strain and resulted in "eradication" of the native Okpo population. Historically, this successful field trial has generated great deal of interest and enthusiasm in genetic methods of mosquito control. Similar incompatibility exists in *Aedes scutellaris* species complex and could also be used for genetic control (Knipling *et al.* 1968).

d: Competitive displacement (Species replacement)

Competition between populations of *Aedes polynesiensis*, a major vector of filariasis in Polynesia and *A. albopictus*, results in elimination of *A. polynesiensis*. This happens both in relatively small, 1 cubic foot cages (Gubler 1970) and in a large walk-in cage, where conditions of the habitat of the two species were simulated (Rozeboom 1971). Two hundred male and 200 female *A. albopictus* were introduced in the walk-in cage which was breeding for *A. polynesiensis* and producing approximately 4,000 *polynesiensis* adults per week. In small confined space, *A. albopictus* males readily inseminate *polynesiensis* females but the eggs are infertile. Such cross insemination sterility was considered to be an important factor in competitive displacement in Gubler's cages. However, in the case of the large, walk-in cage where steady decrease in *A. polynesiensis* paralleled an increase in *A. albopictus* and where after 41 weeks *A. polynesiensis* was reduced to approximately 5% of its original density, Rozeboom (1971) interpreted the replacement of *polynesiensis* by *albopictus* as resulting from "the higher reproductive rate of the latter species, which permitted it to monopolize the ecological niche provided by the large cage". Whatever the exact mechanism, such competitive displacement of one species by another could be used for replacing a vector or an insect pest by a non-vector or an innocuous form.

A preliminary field trial on a small island in the Pacific utilizing this approach and the above mentioned two species was conducted by Rozeboom and Rosen. However, the results were inconclusive (pers. communication). Additional tests are planned.

Such competitive exclusion has been recently applied with success to the control of a green-house population of race B of the Hessian fly, an agriculturally important Wheat pest, *Mayetiola destructor*, by flooding it with the avirulent Great Plains race at a ratio of 9:1 with 4 releases or 19:1 with 2 releases (Foster and Gallun 1972).

The use of translocations (Curtis 1968) and of compound chromosomes (Foster *et al.* 1972) to fix desirable genes, e.g. for disease refractoriness, conditional lethals etc., has been proposed. The purpose of such gene fixation is to replace an insect pest with a desired genotype which in certain cases could be subjected to additional manipulations of insecticidal or climatic control (Klassen *et al.* 1970a).

e: Chromosomal translocations

The use of inherited sterility associated with chromosomal translocations has been suggested for pest control (Rai 1967, Rai and Asman 1968, Rai *et al.* 1970, Laven 1969, Curtis 1968 and Wagoner *et al.* 1969). Although the potential of this method was originally proposed more than three decades ago by a Russian geneticist, Serebrovskii (1940), it was not until recently that its use for a number of insect species, e.g. mosquitoes, tsetse flies and houseflies has been contemplated and progress made.

Among mosquitoes, the potential of chromosomal translocations is being evaluated in *Aedes aegypti* (Rai and McDonald 1971, Rai *et al.* 1972), *Culex fatigans* (Laven *et al.* 1971), *Culex tritaeniorhynchus* (Sakai *et al.* 1971) and *Anopheles gambiae* (Davidson, personal communication).

In *A. aegypti* approximately 40 reciprocal translocations have been induced and cytogenetically analyzed for their break points, fertility, fecundity and their transmission characteristics. Studies are then undertaken on the competitive mating ability of males heterozygous for the more promising of these translocations in laboratory and field population cages (Rai and McDonald 1971) and attempts made to produce homozygotes for such translocations. Similar studies are underway with other mosquito species.

Computer simulations using the available data in *Aedes aegypti* have indicated the potential role of various types of sex-linked and autosomal translocations for genetic control under various release strategies (McDonald and Rai 1971). Using such computer simulations, Curtis and Robinson (1971) have provided important theoretical considerations on the use of various types of double translocations for pest control.

Field work done under the sponsorship of the World Health Organization at their Research Unit on Genetic Control of Mosquitoes in Delhi, India during 1971 showed the genetic incorporation of a male-linked translocation in a natural population and its maintenance for several generations following the termination of the field releases which approximated a single generation span of *A. aegypti* (Rai *et al.* 1972). This was the first demonstration of its type among any vector species. It need hardly be emphasized that such a maintenance of an introduced genotype or sterility condition over several generations will be an essential prerequisite for successful application of any genetic method of control. Laven *et al.* (1971) have also shown incorporation of a sex-linked translocation in a discarded well population of *Culex fatigans*. Releases of a sex-linked translocation were made into this well for two months. As a result, the percentage of semisterile egg rafts increased to "95% or more" and the adult population declined to 90% of its original level at the end of this experiment.

These experiments with *A. aegypti* and *C. pipiens* have indicated that with proper manipulations, it should be possible to use translocations for population control. Additional field work with *A. aegypti* is currently underway at the W.H.O. Unit in Delhi by Rai and colleagues and at the University of Notre Dame field Unit in Mombasa, Kenya, by McDonald.

Lorimer, Hallinan and Rai (1972) have recently isolated two translocation homozygotes (among the forty tested) in *Aedes aegypti* which should considerably enhance the potential of the translocation method for genetic control. The use of these homozygotes for actual control of field populations will be undertaken in Delhi during 1972-73.

Since chromosomal translocations can be induced with relative ease (Rai 1968), their feasibility for genetic control can be evaluated in any pest species. Same is the case with mutagen-induced sterility except in those cases where the sterilizing dose may be close to the lethal dose.

f: Other mechanisms

The use of several other genetic mechanisms, e.g. meiotic drive (Hickey and Craig 1966), dominant conditional lethal mutations (Klassen *et al.* 1970b, Smith 1971), deleterious recessive genes (LaChance and Knipling 1962, McDonald 1970) to suppress insect populations has been suggested. However, the potential of none of these has yet been tested in any trials.

Economics of Genetic Control

It is not my intention to consider the economics of genetic control in any detail, partly because of the paucity of published figures on cost for more than a very few species. Nevertheless, the available figures are suggestive of not only economic feasibility but of considerable economic gains ensuing from successful application of the sterile male method. With genetic control, where considerably fewer individuals may have to be released to effect control, the cost of a successful operation may be considerably less than that of the sterile male technique.

The annual loss to the cattle industry caused by screw-worm infestations in Texas was approximately $100 million and the cost of eradicating the fly about $12 million (LaBrecque and Keller 1965). The cost of the Florida eradication program for the same species was $10.6 million and the savings estimated to exceed 20 million dollars annually (Bushland 1971). In order to prevent immigration of this fly from Mexico to the United States, USDA releases an average of 125 million sterile males each week along a buffer zone along the Mexican border. Currently, "the annual cost of the screw-worm program is one-fifteenth of the estimated annual losses due to the control costs and live stock damage before the insect was eradicated. Knipling's price tag on the cabbage looper program is $2.5 million a year, less than the cost of developing a new insecticide and he says that control of the boll weevil alone would pay for all other pest control programs combined" (Holcomb 1970).

With traditional methods of insect control, e.g. with insecticides, the cost per year remains the same. With genetic methods, the cost may be relatively high in the first year but may be much less for subsequent years to maintain quarantined control. *Heliothis zea* causes economic losses of approximately $400 million per year in the U.S. (Knipling 1969). He has estimated that 80 billion sterile moths could be produced with the same amount. The chances are that "it may require far fewer than 80 billion moths to maintain suppression below the economic damage level even during the first year" (Knipling 1969). LaBrecque and Keller (1965) have provided many additional estimates of the costs of insecticidal, sterile male and integrated control.

CONCLUSIONS

The original screw-worm saga has opened up the new field of genetic manipulation of insect populations. The application of such manipulations for controlling insect pests is briefly surveyed. Certain important principles underlying genetic control mechanisms are emphasized and field trials involving some of these mechanisms undertaken to date, particularly with various mosquito species, are briefly discussed. Data from some of these field trials are encouraging.

Although considerable progress has been made in this area during the last decade, important frontiers yet remain to be conquered. Considerably more basic research needs to be done, not only with the development of such mechanisms and their field testing, but with various aspects of field biology, ecology and dynamics of the target field populations. In addition, critical information will be indispensible concerning (a) the selection of the genetic composition of the material for releases, material which has the best chance of accomplishing the set goals of control, replacement etc. (Lewontin 1965, Remington 1968, Lucas 1969, Whitten 1970, Mackauer 1972); (b) the behavioral aspects of mass rearing (Boller 1972); and (c) development of relatively inexpensive methods for mass production.

Perhaps the most important criteria that will often determine whether a genetic manipulation succeeds or fails would be that the various components of the behavior of released insects are not significantly different from those of the native population, that the former are derived from the latter in the not too distant past and that both have similar genetic composition encompassing the same spectrum of genetic variability, thus assuring that the matings are random between the two. Obviously the best genetic technique in the world will not do anyone any good if adequate regard is not paid to such criteria and to assuring the quality control of mass-reared insects such that ethological differences among the released and native populations do not come into play. As mentioned earlier, such difference might produce negative results from an otherwise worthy technique. Experience from field trials of the sterile male technique with mosquitoes is surely instructive.

Nevertheless, the prospects for the application of genetic methods of control in relatively small scale, isolated locations appear quite good. Additional field trials in relatively large test sites are badly needed. The work currently underway at the W.H.O. Unit in Delhi, India, on the feasibility of such methods for mosquito control should tell us, relatively soon, as to what extent such methods could be used for operational control of insect populations. Because of the high population densities which characterize most insect species and the necessity of flooding such populations with introduced genotypes, the best approach for insect control would have to involve integrated control whereby the original population densities are drastically reduced by a whole host of traditional methods and the genetic methods are used as the ultimate weapon. Furthermore, if genetic methods are developed in insecticide resistant strains, insecticidal treatments could be continued even after releases. This way relatively small releases could be quite effective (Whitten 1970, Wehrhahn and Klassen 1971).

Of course, in a country like Canada with a massive land mass which is sparsely populated and has a diversity and alarmingly high population densities of biting flies, the prospects of the application of any known genetic method for operational control in the near future are minimal. The specificity of the genetic control would surely tend to limit it for any large scale applications for anything but a few species. Until such species are important disease vectors or cause huge losses to the economy of a region, it is unlikely that the genetic methods, in view of their cost, will be considered seriously for operational application.

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DISCUSSION

Discussion Leader	**J. R. Anderson**
Discussants	**B. V. Peterson** **G. O. Poinar, Jr.** **M. Laird**

Peterson: I would like to commend Drs. Bay, Chapman, and Rai, for their fine presentations. There are so many points of concurrence among us that the task of discussion is made rather difficult. Being a systematist and really little more than an interested outsider, also puts me at a disadvantage in making some useful comments. However, being a systematist, as well as a bit of the old type of field naturalist, has provided me with many opportunities to see diseased and parasitized biting flies, both at the laboratory bench and in the field while collecting and observing biting fly behavior. Each time I see or collect an afflicted specimen I wonder why I don't see more of them, and why some are affected but the apparent majority are not, and if the numbers I see are really indicative of the situation as it occurs in nature or if the afflicted individuals really are, or were, somewhat or vastly more numerous and perhaps have died thus leaving a false impression of the effectiveness of these natural enemies. A similar set of questions can be posed in regard to the predators of biting flies. Perhaps some of our speakers might wish to comment on these queries. However, it is doubtful that anyone can really answer these questions since, to my knowledge at least, such studies are very few or have not been undertaken.

It is surprising that no one has given a definition of the term biting fly as it pertains to this symposium. There are about 15 families, of the 105 or so in the Order Diptera, that during one stage or another of their life cycles feed on the blood of man or other animals. However, I believe we are primarily concerned with the six families in Canada having man-biting flies; these and their approximate number of Canadian species are as follows:

Culicidae with about 65 species
Simuliidae with about 120 species
Tabanidae with about 135 species and subspecies
Ceratopogonidae with about 380 species
  Culicoides with about 15 man-biting species
  Leptoconops with 2 man-biting species
Rhagionidae with about 9 biting species (i.e., *Symphoromyia* spp.)
Muscidae with 1 biting species (i.e., *Stomoxys calcitrans* (L.)).

Then there is the non-biting but scarifying-sponging-sucking genus *Hippelates*, Family Chloropidae, with about 5 Canadian species. Not all of the species in these families are man-biting; some we know are non-biting, some are bird or mammal feeders, and for many of the other species we can only guess about their feeding habits. I would like to comment briefly on some of the insect parasites of some of these biting flies, an area largely ignored by our speakers.

Dr. Bay has already mentioned the hymenopterous egg parasite of Tabanidae, *Phanurus emersoni* Girault (now *Telenomus emersoni*) and cited as reference the classic paper by Parman (1928). Papers previous to and after that of Parman, including works by Webb and Wells (1924), Cameron (1926), Philip (1931), Miller (1951), James (1952, 1963) and Teskey (1969), have all reported various species of several genera of Tabanidae to be parasitized by hymenopterous species among which are *Telenomus emersoni* (Scelionidae), *Diglochis occidentalis* Ashm. (Pteromalidae), *Trichogramma minutum* Riley (presumably *T. semblidis* (Aurivillius)) (Trichogrammatidae), *Anaphoidea* sp. (not *Patasson* sp. (Peck, pers. comm.)) (Mymaridae) and *Trichopria* spp. (Diapriidae). Jenkins (1964) lists at least eight additional hymenopterous parasites of Tabanidae from other parts of the world which have varying importance as biological control agents.

Other insect parasites of tabanids mentioned in the literature include the Tachinidae and Bombyliidae. The tachinid *Carinosillus tabanivorus* (Hall) is a parasite of tabanids (Philip 1931; Hays 1958), and this genus contains at least two other species, represented in the C.N.C., which are possibly tabanid parasites as well (Wood, pers. comm.). Another tachinid, *Phasiops flavis* Coq., is a tabanid parasite, and there is a third genus, *Opsotheresia*, which might prove to have species parasitic in tabanids. Jenkins (1964) also lists *Vibrissotheresia pechumani* Reinhard as a tabanid larval parasite, and James (1963) lists *Carinosillus novaeangliae* (West) (as *Phorostoma novaeangliae*) as a larval parasite. However, according to Wood (pers. comm.) the taxonomic positions of some of these species are uncertain. Here we are faced with the not unique situation of having an inadequate knowledge of the taxonomy of a potentially important group of parasitic species. This also applies to the parasitic hymenopterous species mentioned elsewhere. The bombyliid, *Villa lateralis* Say, has been found to be a tabanid parasite as well (Teskey, 1969).

Turning briefly to the Simuliidae, Peterson (1960) reviewed the hymenopterous insects reported to be parasitic in black flies. He observed an undescribed species of the *Telenomus basalis* Wollaston complex (Scelionidae) emerge from the abdomen of the black fly, *Simulium* (*Gnus*) *arcticum* Malloch. This might have been an accidental occurrence because species of this group of *Telenomus*, whose habits are known, are parasitic in the eggs of certain Hemiptera. All previous records of hymenopterous parasites in black flies are Old World and include two braconids from *Simulium* (*Eusimulium*) *aureum* Fries, *Ademon decrescens* (Nees) and *Gyrocampa affinis* (Nees) (now *Chorebus affinis*) (Enderlein, 1921). These records however are suspect. Planidia larvae, apparently belonging to the genus *Perilampus* (Perilampidae), were found by Lewis (1952) in the heads of male and female *Simulium* (*S.*) *damnosum* Theobald from the Sudan.

It is interesting to note that between Peck (1963) and Jenkins (1964), about seven hymenopterous parasites are listed from *Stomoxys calcitrans*, but no insect parasites are listed for the Culicidae, Ceratopogonidae or Rhagionidae. However, that doesn't mean there aren't any such parasites for these families of biting flies. Perhaps some of our speakers would care to comment on this anomaly or have more recent knowledge on this topic they could share.

Parasites of biting flies other than those discussed by Drs. Bay and Chapman and the insect parasites just mentioned, apparently are not very numerous or are so effective as control agents as to be rarely collected (this latter possibility is remote). Records of such parasites include: *Planaria* sp., mites, and trematodes (Lewis and Wright, 1962) in the Simuliidae; Rotatoria, trematodes and mites in the Culicidae; and only mites in the Tabanidae, Ceratopogonidae and Muscidae (*S. calcitrans*) (I didn't bother to explore such parasites of the Rhagionidae).

Immature and adult biting flies often fall victim to various predatory organisms. In the field I have witnessed numerous instances of such predation, especially among the black flies, and the literature is replete with similar observations. As Dr. Bay has already pointed out, Jenkins (1964) recorded more than 900 predators of medically important arthropods, and that most of these records are simple host-predator observations made either in the field or in the laboratory. With the possible exception of the larivorous fish, such as *Gambusia affinis*, few if any definitive studies have been conducted on the over-all and lasting effectiveness of biting fly predators. Undoubtedly, there are times when such predators are instrumental in significantly reducing local populations of some biting flies, but, unlike the parasites of these flies, the chances of regulating more than a few suitable predator-prey relationships are very remote. About the best we can do is be thankful that such predators exist to take what portions of the biting fly populations they do. I would be interested in the opinions and experiences of our speakers or others who might be involved with this type of investigation.

We know from personal observations and various reports in the literature that some natural enemies can and do constitute effective biological control agents of certain species of biting flies in various places at various times. However, their effectiveness in nature is certainly not always constant, often varying considerably from place to place and from time to time. It seems to me that the effectiveness of these agents is going to remain generally minimal until some very basic biological studies are conducted to help determine why they are effective under certain circumstances but minimally so under other conditions. As with too many other things, I think we often put the cart before the horse, and expect, or hope to receive revelation or nearly instant answers without doing the necessary homework; even for revelation we must first do our part before the Man-On-High will do his.

Although the potential is high, there is yet little to be had in the form of effective biological control agents for biting flies. Difficulties in harnessing these agents are many particularly since we know so very little about the ecology of either such potential agents or their intended victims. In 1955, Pepper had this to say, "Without a knowledge of the true relationships of both the host and the enemy to their environment as well as an understanding of the interrelationships between the two populations, there is no basis for postulating any effects, either detrimental or beneficial, of parasites or predators on the host populations". And, from a conference on biological control held in 1960 under the joint sponsorship of the American Institute of Biological Sciences, the United States Armed Forces Pest Control Board, the Office of Naval Research and the Army Chemical Corps, came the following statement: "Pathogens, parasites and some predators offer a real potential for natural control of medically important insects. Tests and experiments to date have shown promise, and have also demonstrated the absolute requirement for basic knowledge of the ecology and life history of the pathogens, parasites, or predators, and insect hosts".

Despite the extensive literature, it appears there is a tremendous lag in the knowledge and development of biological control as compared to control by insecticides probably because of its more exacting nature, and higher costs in terms of time and labor, for the returns obtained. It also seems apparent that effective and repeatable biological control measures against biting flies will remain rather distant until advances are made and reliable data are obtained in respect to the ecological factors mentioned earlier. Although a considerable amount is now known about some of these factors, there is need for a great deal more research. My question now is, where do we go from here, and how are we going to get there?

Although there probably are as many definitions of biological control as there are workers in the field, I would guess that most workers adhere to the rather broad concept as advocated by such eminent authorities as Stern *et al.* (1959) and DeBach (1964) who define biological control as, "the action of parasites, predators, and pathogens in maintaining another organism's population density at a lower average than would occur in their absence". This concept is taken to mean just what it says, the use of natural enemies to regulate the numbers of a pest species. But to what category do such control procedures as the following belong: 1) Alterations in the fauna that affects the food supply and shelter of biting flies or other pest species. 2) Alterations in the flora that affects the food supply and shelter of pest species. 3) Alterations in the flora that might affect the food supply or shelter of some stage of the predator or parasite fauna of pest species. 4) Alterations in the physical conditions of the environment that might affect either the pest species or their predators or parasites. 5) Genetic manipulation of pest species. 6) Use of chemosterilants on laboratory reared pests for field release, or in baits for such pests. 7) Use of traps baited with synthetic attractants. 8) Use of synthetic juvenile hormones as insecticides. 9) Use of bacterial toxins. 10) Use of sound as an attractant; etc. etc.

Perhaps it would be well to reiterate the question posed by Breyev (1971), "What is a biological method of control and in what sense is it biological?" Do we now need a broader definition of biological control than the one quoted above? It seems that this might give a lot more leeway in soliciting funds for studying the various facets of biological control than the mere seeking out, raising and releasing of potential pathogens, parasites and predators of biting flies and other pest species.

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DISCUSSION

Poinar: I would like to thank the speakers this morning for their very interesting presentation and discuss some biological control measures that were not mentioned by them.

Recently, Dr. Eldon Reeves discovered a *Bacillus* from local populations of *Culex* in canyon areas in Southern California. He discovered that this bacterium was especially pathogenic to species of *Aedes* and sent it to the Pasture Institute for identification. It was identified as belonging to serotype I of *Bacillus thuringiensis* var. *thuringiensis*, although it was obvious that it was different by possessing 2 crystals (instead of one) lacking the fly factor and being pathogenic to mosquitoes. Cultures were sent to International Minerals and Chemicals in Libertyville, Illinois and they prepared an emulsifiable concentrate that could be used in the field. Field tests are in progress and with the excellent results obtained using *B. t.* against agricultural pests, this product looks promising and should definitely be tested further. Interested persons can write to I. M. C. and obtain samples of the bacterium for experimental tests.

Dr. Reeves is also working with the higher algae, *Chara* and the filamentous green algae, *Cladophora*, both of which produce substances toxic to mosquito larvae. An extract has been obtained from these plants which is active against *Aedes* spp. and *Culex* spp. and tests are currently being conducted to test the effectiveness of this compound.

At Berkeley, Dr. R. D. Sanders has been conducting a survey on the pathogens of *Aedes sierrensis*, which constitutes a serious problem in its range. Aside from discovering a new species of the protozoan genus *Pleistophora* and *Lankesteria*, Dr. Sanders has also found several more promising pathogens. In 4 of the 18 treeholes sampled, 26-90% of the mosquitoes were infected with the fungus, *Beauveria tenella*. This fungus invades the siphon and gut and eventually kills the larva. Dr. Cubbin of our Department is growing the fungus on agar plates and in broth for further testing. Spores isolated from the cultures were infective to *Aedes dorsalis*, *A. aegypti*, *A. hexodontus*, *Culex pipiens*, and *Culiseta incidens*. First stage larvae of *A. aegypti* were extremely susceptible and 86% mortality resulted in third stage larvae. Preliminary field trials have been conducted with promising results.

Interested persons wishing to obtain a sample of this fungus for infectivity studies can write Drs. Chris Cubbin or D. Sanders.

A mermithid nematode was also found parasitizing larvae of *A. sierrensis*, but it was found in only one treehole and only 32 larvae out of 320 were found infected. However, we are attempting to obtain enough material to initiate a breeding program for field releases. The larva dies soon after the nematode emerges.

Dr. Richard Garcia has been investigating predators of mosquito populations. He recently discovered that the small hunting spider, *Pardosa sternalis* (Thorell) may be an effective predator of *Aedes dorsalis* in salt marshes. The spider attacks the adult mosquitoes as they emerge from the pupal case and move toward the surrounding vegetation. They could also pick up mosquito larvae and pupae in laboratory experiments. Dr. Garcia has also been investigating the possibility of using notonectid bugs for controlling mosquito larvae in temporary pools. He finds these bugs very efficient predators and has now devised a method of breeding them under laboratory conditions. Harvesting the eggs and releasing them in temporary water sources is currently under intensive investigation.

In all the above cases, we are departing from the traditional example of biological control where an exotic parasite, etc., is brought in to be released against a particular pest. Here, we believe that the natural agents can be very effective if introduced in large enough numbers. Thus, by mass producing these naturally-occurring agents and distributing them in the environment, pest populations can be reduced.

We still need to know why these natural agents occur at such low levels in nature and current investigations should be directed along these lines.

Laird: At the conclusion of a preliminary survey of Edmonton's gastronomic possibilities last night, my fortune cookie contained not one but two slips lettered "Highlight imagination, original approach". So here goes, in hopes that a discussant's licence at this Symposium extends to previous sessions where relevant; and in full confidence that everything important has already been said, anyway, by the readers of those three excellent papers this morning and by the two preceding discussants.

For one message came through to me, loud and clear, from yesterday's session – that chemical control, biological control, third generation pesticides control and the rest, are all misleading phrases which severally hold out hopes of altogether illusory panaceas or imply disciplinary cleavages that should never have been allowed to exist. Whether our individual interests centre upon the chemical control weapons to hand at this moment, future hormonal or genetic control procedures, or the impending development of marketable biological control procedures that really work, there must be few among us who don't recognize that tomorrow's approach to biting fly control is going to be an *integrated* approach – one in which chemical, biological, mechanical and other procedures are going to be used conjointly, against a background of exhaustive ecological understanding of the target pest or vector, and in methodologies combining maximum selectivity and effectiveness with the irreducible minimum of undesirable side-effects upon non-target organisms. Hopefully, too, these methodologies will not saddle us (especially those of us who live in the less affluent countries or the poorer regions of so-called "developed" nations) with overly expensive bills to pay. Hopefully, again, by the time, perhaps a quarter of a century from now, when we are ready to put integrated control methodologies to work against biting fly pests and vectors on a widespread basis, we will have seen to the training of the necessary numbers of appropriately qualified entomologists who will be needed to *implement* such methodologies. *Point One – Biological control is not going to be an end in itself but is and will remain a component of integrated control, firmly based upon an enlightened biological approach.*

Yesterday morning, Dr. Maurie Provost quoted Aldo Leopold's apt remark about the danger of the PhD's becoming "as callous as an undertaker to the mysteries at which he officiates". He also, incidentally, mentioned whooping cranes, which have become one of the most frequently quoted examples of an endangered species, pushed to the wall by man's technological juggernaut crushing its way towards an ever-higher GNP. I think I can claim to have thought and worked as an ecologist since before ecology showed signs of becoming a religion – and like many others in this room I both like whooping cranes, moas and dodos; and recognize that extinction has always been a necessary part of the evolutionary process. Being human, we tend to take a tender interest in the beautiful losers while ignoring the scruffy and ubiquitous success stories like house sparrows and dandelions. So we condone the spending of millions of dollars upon research pertinent to the last small handful of whooping cranes, while turning a blind eye to the whittling away of the USDA's biological control strength, the Canadian Armed Forces' entomological strength and the parsimonious funds presently made available by governments for R & D towards more effective and selective biting fly control. Perhaps one solution might be to apportion government allocation of the taxpayer's dollar to more realistic goals than those sometimes selected. There might, for example, be more money available for research towards integrated control in public health entomology if we did as one cynic has suggested and allotted a fraction of what we're now spending on those last whooping cranes to the goal of teaching ordinary cranes to whoop. *Point Two – We need more financial support.*

Seriously, though, Dr. Brian Hocking's urging that we incorporate more and better entomology in curricula with better biological content, makes a great deal of sense. And I would hope that the entomological community a quarter of a century from now will contain a higher percentage of old-fashioned observers than the present one does. New modelling and other techniques have at one and the same time opened a door to the future and caused many of us to forget the already-old saw about computers – "garbage in, garbage out". Also, recent preoccupation with monofactorial laboratory experimentation as a basis for free extrapolation, has produced a disquietingly large number of highly specialized but narrowly experienced entomologists. Some of these, if put to the test, would experience difficulty in distinguishing between anopheline and dixid larvae. They might also prove reluctant to leave air-conditioned laboratories and risk getting all muddied up in the field. *Point Three – The biological component of integrated control and indeed the whole future of biting fly control demand more and ever-better entomologists.*

It has been encouraging throughout this meeting so far to hear so many contributors speaking from experience about the continuing need in biting fly control for DDT – the lack of which would represent a severe setback to vector control in developing countries still struggling with malaria, onchocerciasis and other such diseases. Also, it is worth recollecting that the latest edition of the International Health Regulations, issued by WHO in 1971, lists only three formulations as acceptable for this facet of international quarantine activity. Two of these formulations, one of them the Standard Reference Aerosol, contain DDT. Moreover, in my view, the efforts of some environmentalists to have DDT banned represented a real body blow to integrated control. For if we're ever going to develop practical integrated control methodologies that can be depended upon for depressing vector populations to the point where disease transmission (whether to man, domestic animals or wildlife) ceases, we're going to have to have available, for selective use as required, the widest possible selection of weapons in our armoury. There will be occasions and situations where a relatively cheap, unusually safe and highly persistent pesticide like DDT will be an essential component of integrated control methodologies. Surely, then, one of the major challenges facing us is to find ways of ensuring that we derive maximum benefit from all the control options available to us, including DDT, with the absolute minimum of undesirable side-effects. This is going to demand hard, slogging efforts on all our parts towards more and more selective field application techniques implemented under more and more effective (and effectively enforced) regulations based upon solidly scientific criteria for environmental quality. *Point Four – Biting fly control in all its aspects (biological, chemical, mechanical, and the rest) is going to have to be conceived, implemented and monitored under wisely legislated regulations.*

I think it was Dr. Al West who remarked that 'we need standards for biting fly control practice such as those already in existence for spruce budworm control. The landing rate of blackflies was mentioned as one such standard. With all due respect Al, standards (a basis for regulations) are themselves founded upon scientific criteria, a criterion being a basis for judgement. In the area of biting fly ecology and vector-borne disease epidemiology, we have scarcely begun to explore such criteria. Without them, we're only name-dropping, as it were, in talking about biological control as an ingredient in integrated control. For example, how do we assess the gravity of a biting fly pest problem? Usually, I suspect, we do it on the basis of heavy mosquito, blackfly, or tabanid attack on town-based people experiencing their first-ever, or first-of-the-season, such exposure to these insects. Especially in the more northern areas where biting flies are most prevalent, we seldom bother to ask local people whether they regard a particular incidence of biting flies as constituting a pest problem. We forget, too, that (especially in these same northern regions) ornithophilic blackflies and mosquitoes spread blood parasites to wildlife. Avian malaria caused by species of the genus *Plasmodium* and spread by mosquitoes, and leucocytozoonosis spread by blackflies thus suggest themselves as possible biological criteria relating to the better definition of biting fly pest and vector problems. For example, can we hope one day to be in a position to say that incidences of particular avian haematozoa above particular levels constitute a health hazard to wildfowl populations, and that such incidences can be used, together with more precise evaluations of pest situations from the human standpoint, as scientific criteria for standards and regulations determining just when integrated biting fly control measures should be implemented? I suggest that we can. *Point Five – We need scientific criteria, including biological (and perhaps sociological) ones for the development of a sounder range of standards in our field.*

The Status of Biological Control in Medical Entomology

Leaving the potentialities of genetic control to somebody more competent than I to deal with it, and observing that mosquitoes and blackflies are unhappily free from the entomophagous insect parasites that have proved so useful in economic entomology (despite the facts that there *are* scattered records of tiny hymenopterous parasites of simuliids, and a mention of *possible* entomophaga from mosquito eggs), I propose to consider only two aspects of biological control in this discussion – both of them as ingredients in integrated control. First of all, the role of predators must be recognized. Our only real success story in the biological control of mosquitoes (setting aside Dr. Hocking's purple martens and Dr. Campbell's Malaria – Eradicating Bat Roost*, concerns larvivorous fish. The best known of these are the guppy, *Poecilia reticulata* and *Gambusia affinis*, the top minnow. *Gambusia* has already been mentioned in this symposium, interestingly enough never beyond the specific name of "*affinis*". There are in fact subspecies of this fish, but it's a long time since I heard any mention of possible differences in behaviour and feeding patterns between *Gambusia affinis affinis* and *Gambusia affinis holbrooki*. The extensive literature on mosquito fish doesn't tell us very much, either, about which subspecies was introduced where in the 1920's and 1930's. But some recent papers by Myers, Alwyn Wheeler of the British Museum and Hurlbut and others suggest that "*Gambusia affinis*" has, through possessing much more omnivorous propensities than was popularly supposed, had long-term *adverse* effects upon aquatic ecosystems. Myers and Wheeler have indicated that mosquitofish have disrupted populations of economically and aesthetically desirable indigenous fish. Hurlbut and his co-workers (in SCIENCE for 11 February of this year) have demonstrated that by greatly reducing herbivorous zooplankton *Gambusia* predisposes towards phytoplankton blooms and so contributes towards eutrophication – just like all those nasty chemical effluents. *Point Six – Before embarking on field introductions of biological control agents against mosquitoes and other biting flies, we must obtain much more exhaustive baseline information than we have done up to now on the total ecology of the ecosystems (especially aquatic ecosystems) harbouring those life-history stages of our target pests or vectors selected for attack: and we must be very much better informed than we have usually sought to be in the past on the ecological parameters of our chosen biological control agents. In parentheses we should be paying attention to bettering our taxonomic standards in this context, too.*

Point Seven – We need more candidate parasites and pathogens for consideration of their biological control potential. The means of obtaining such material is already in operation via the World Health Organization's global survey featuring the now well-known pocket kit and Dr. John Briggs' WHO international reference centre for diagnosis of diseases of vectors (at Ohio State University).

Point Eight – is closely related to the last two Just as we have a duty to ensure that we use chemical pesticides in so selective a way as not to pose significant hazards to the health of man, domestic animals and wildlife, so must we ensure that candidate microbial control agents – be they viral, bacterial, fungal, protozoal or helminthic – do not endanger health either. Not enough work has been done in this field and scarcely any as regards three leading candidate microbial control agents in public health entomology – mermithid nematodes, microsporidan protozoa and *Coelomomyces* fungi. This was emphasized by a symposium of the 4th International Colloquium on Invertebrate Pathology at College Park, Md., in 1970 and re-emphasized by a symposium of the first European Multi-Colloquy of Parasitology in Rennes, France, last fall. Also, a Working Party of the Society for Invertebrate Pathology has been formed to explore further relevant research needs and priorities.

Finally, what about the present availability of microbial control agents? There seems to be widespread agreement that these constitute our best hope for the biological control of biting flies, at least in the reasonably near future. Well, despite some promising field trials, we can't yet mass-produce microsporidans or *Coelomomyces*. The prospects for mermithids of mosquitoes look good, though, and collaborative studies towards the mass cultivation of mermithids of blackflies, as well as of microsporidans and *Coelomomyces*, are being planned in Newfoundland (which for Ernie Bay's benefit is not all that far north). For Harold Chapman's advice, I registered his point about my finishing off my section of a joint paper on a *Coelomomyces* from Louisiana *Toxorhynchites*. This is a particularly interesting association. It features one of the leading candidate pathogens for eventual use against mosquitoes, destroying what some people feel to be one of the leading candidate predators for eventual use against mosquitoes.

Point Nine – It's necessary to solve this problem of mass-producing these organisms to open the way to industrial R & D and scaling up, against the day

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*Campbell, C.A.R. 1925. Bats, mosquitos and dollars. Boston, Stratford. 262 pp.

when it becomes profitable to market Coelomomyces, microsporidan and mermithid concentrates able to give results in the field in accordance with their use following instructions on the label. Then, and only then, is biological control likely to attain its rightful place in integrated control. Like Dr. Rai, though, I'm an optimist at heart and with him can see that light shining at the end of the tunnel.

I'd be prepared to gamble on some exciting results within five years, granted reasonable support.

Anderson: In closing the discussion I first wish to thank the three speakers who addressed us this morning and the discussants whom we have just heard. Although the discussants admirably covered a number of significant points, unfortunately for me little has been said up to this point about the potential for genetic control of biting flies. I know little about this field myself, but I do have some questions I would like to ask. The first question concerns the possibility of univoltine northern *Aedes* species having heterogonic eggs in which perhaps only 20% of the eggs in each clutch would hatch after a given flooding. Since this is the case for many salt marsh mosquitoes at least, I wonder whether in such instances one would have to release an alien genotype into these populations for something like five consecutive years to achieve the population reductions Dr. Rai postulated.

In his slides Dr. Rai showed eight potentially useful mechanisms for genetic control of mosquitoes, but I wonder if there might not be a ninth possibility in autogenous strains which might act as competitive ecological homologues of anautogenous strains. In summarizing the results of about ten field trials in which genetic control of four mosquito species was tested, I believe Dr. Rai listed four of the trials as being successful. In view of the limited time Dr. Rai had to present his data I do not wish to be overly critical or conservative, but before we accept his evaluation of these field trials, perhaps we should hear more about what criteria were used to judge whether or not the trials were successful. I also would like to know if the methodology was practical, if it is being used now, and if there are plans for large scale releases. Do the test areas, for example, no longer have a mosquito problem? Another reason for these questions regarding genetic control is that the current large influx of screw worms (e.g. U.S. Dept. of Agric., Coop. Econ. Insect Rpt. 22:214,271) into Texas and adjacent states has aroused my curiosity. In view of the large numbers of flies involved, I wonder if anyone in the audience knows if a Mexican genotype is behaving differently, or what the explanation for this current outbreak might be?

The other point that struck me about Dr. Rai's presentation was his slide of the huge pile of tires and its relationship to the *Aedes aegypti* problem. I must say that almost every time I have heard an *Ae. aegypti* problem discussed, I have seen similar pictures showing a mountain of tires which was identified as a major source of the problem. Following the dengue outbreak in the Caribbean islands a few years ago, I saw at meetings slide after slide of such piles of tires, and when my colleague, Dr. McClelland, returned from Africa a year or so ago, I saw slides of more piles of tires; again this morning I saw more slides showing piles of old tires! It certainly seems to me that the W.H.O. and other organizations are missing the fundamental solution to the control of *Ae. aegypti* and the pathogens vectored by this species by not supporting research projects on the potentialities of recycling old tires. Also, there perhaps might be a better cost-benefit return associated with the recycling of used tires. The elimination of breeding sites by recycling used tires probably would not cost as much as other practiced methods of control and it also would represent a permanent solution to the problem. Sometimes man's approach to solving problems makes one wonder whether we really want to solve the problems.

Dr. Laird mentioned use of the mosquito fish, *Gambusia affinis*, and Dr. Bay commented on the use of *G. affinis* in rice fields near Fresno, California, U.S.A., by Hoy & Reed (1971). Dr. Bay pointed out that Hoy & Reed (1971) reported acceptable control of *Culex tarsalis* by introducing only 100 gravid female fish per acre. I would like to point out, however, that at times fish also can create a mosquito problem, at least a temporary one. For example, Hoy, et al. (1972) found that in rice fields near Sacramento, California, U.S.A., a stocking rate of 0.2 lb. (100 fish) per acre resulted in a significantly greater number of mosquito larvae after one month in stocked fields than in untreated check fields. Fields stocked at 0.6 lb. (300 fish) per acre had significantly fewer larvae than check fields (18 replicates of each). As fields receiving only 100 fish/acre had significantly more mosquito larvae, it appears that the fish indiscriminately feed on all invertebrates present, including various predators. After a month the fields receiving 100 fish/acre showed considerable reductions in the numbers of mosquito larvae present. In California rice fields mosquito fish thus seemed to cause an adverse disruption in the indigenous invertebrate predator populations. Dr. R. Washino (in press, Proc. Calif. Mosq. Control Assoc., 1972) has found some interesting correlations between numbers of mosquito larvae in rice fields and numbers of arthropod predators. The other interesting point in the paper by Hoy *et al.* (1972) was the evidence for resurgence of the *Culex tarsalis* population in rice fields after being treated with an insecticide. The fields were treated the second week of June and by mid-July a marked resurgence was already in effect. In July and August all the fields that had been treated in June had larval populations that were significantly greater than those in the untreated checks.

One suggested measure for increasing insect predators in rice fields in California (Hoy, J. B., pers. comm.) is the use of large, bright lights to attract beetle and bug predators into rice fields to prey on the mosquito larvae there. However, in rice fields, fish *might* be easier to *manage* than arthropod populations. At least once they are in the fields they tend to stay there instead of flying away as the mosquito larval populations decline. This seems to be one advantage fish have over insect predators.

Although it may be only a rather minor point, I cannot agree with Dr. Bay's historical account of the development of biological control methods for flies of medical importance in California. I would look at numerous events occurring prior to 1961. In fact, one could go back as far as the early use of *Gambusia* by Herms (1928). Nevertheless, historical events aside, in spite of all the research conducted on the natural enemies of filth flies in California and elsewhere (e.g. Anderson 1965, Axtell 1970, Legner & Bay 1970, Legner & Brydon 1966, Peck & Anderson 1969, Wicht & Rodriguez 1970) only integrated (not simply biological) control programs have proved at least partly successful.

When Dr. Bay compared monocultures with natural ecosystems it seemed to me that he implied the former were rather simple systems, but I would like to point out that monocultures are not necessarily simple ecosystems. There may be nearly 100 species of arthropods (Anderson 1964), for example, associated with a modern stretchwire poultry ranch in California – by no means a simple ecosystem. Even the large monocultures of cotton and alfalfa in California support a diverse insect fauna (van den Bosch & Hagen 1966).

Several people already have mentioned that the development and release of pathogens, in many cases, is first going to depend upon our being able to colonize various pest species. Unfortunately, thus far this has been largely unsuccessful with univoltine species, except for a very few species of mosquitoes. Another point to be dealt with is that large scale field tests are needed to evaluate some of the more promising pathogens. Fortunately, Peterson and Hoy currently are conducting a field test with a nematode parasite of mosquitoes in California (Hoy, J. B. pers. comm.). Perhaps Dr. Chapman will elaborate further on this test.

One point I have long been curious about and previously asked Dr. Chapman about, is that in field collections one finds rather typically, I think, low percentages of insects infected with pathogens. Is this because the predators selectively eat the infected, "sick" individuals? I am not aware of any research that has been concerned with this possibility, but if this is the case, I wonder what one would gain by encouraging both pathogens and predators. This might, in fact, represent a situation analogous to mosquito fish and various insect predators in rice fields. Another point of concern associated with the release of exotic microbes is that we should be as certain as possible these will not displace the indigenous bioregulatory species in a super first year. For example, if the introduced pathogen initially caused 90% mortality or more in a host population and then the pathogens themselves were eliminated by unfavorable climatic conditions in a subsequent year, how would the pest species respond in subsequent years if its natural enemies had been displaced? Another point I wonder about is the effect of various pathogens on non-target organisms. Dr. Laird mentioned that microbial control agents used for biological control should not endanger health, but I also think we are just as obligated to determine that such pathogens have no adverse effects on non-target organisms other than man as we are for pesticides.

Another question we probably should ask ourselves today is, to what extent is there duplication of research effort? And another question might be, who are we developing these control techniques for? For example, I recently saw a television program on California agriculture which emphasized that because of automation, corporation farming, etc., $^2/_3$ of the eggs in California are produced by six to eight ranches. If such poultry ranches are having problems with pest flies for example, one wonders about the traditional concept of the state experiment stations associated with universities and the types of problems which should receive priority from its employees. Does anyone other than those few individuals or corporations stand to benefit from the research of experiment station and state health department entomologists? Also, along somewhat similar lines, is the expertise and considerable time of university and experiment station entomologists devoted to past and current testing and evaluation of commercial pesticides analogous to governmental subsidy of other programs. A final point perhaps, is that I sometimes wonder about which species receive our research efforts. In California for example, we have three important mosquito species, *Anopheles freeborni* and *C. tarsalis* in rice fields and *Ae. nigromaculis* in irrigated pastures. The latter two species loom as real threats to man's welfare because they now are resistant to so many insecticides in many areas of California (e.g. Womeldorf et al. 1971). Despite the pressing importance of these three species, considerable research has been conducted in recent years on the tree hole mosquito, *Ae. sierrensis*, and other minor pest species, while perhaps not enough has been devoted to the major pest species. Although this research is interesting from an academic viewpoint, I wonder about the practical point of view at times, and why we sometimes seem to avoid the difficult species causing problems of an immediate nature. In the case of species like tree hole breeders; one wonders how much information would be applicable only to other species breeding in tree holes, and in how many areas of the world tree hole breeders are really important?

Dr. Provost mentioned that manipulating soil and water was basic to farming and he stressed that improvements in agronomy and range management also solved pest problems. I wish this were always true, but in California and a number of other areas I am familiar with, all or nearly all of the biting fly problems and the other fly problems of today seem to have resulted from man's manipulation of natural ecosystems. Perhaps such changes cannot be considered "improvements", but in any event, they include manipulations related to modern agriculture and to current living conditions, and recreational areas. In my view these manipulations seem to have caused or changed our insect problems. The major biting fly problems in California are represented primarily by mosquitoes, species that are associated with irrigated pastures and rice fields. Years ago the salt marsh mosquito problem was largely solved by habitat manipulation, but since then agricultural practices in the central valley have created other serious mosquito problems. Another biting fly problem we have, is that of *Stomoxys calcitrans*, whose abundance is due to such current agricultural practices as cattle feedlots, slatted calf pens and stretch-wire poultry ranches. In California, problems like this and the hordes of mosquitoes produced as a by-product of man's manipulation of an ecosystem (e.g., irrigation of fields or construction of reservoirs) are being considered more and more as pollutants in the same sense as chemical pollution of water or odor pollution of air. At the same time however, the hordes of mosquitoes that often eminate from salt marshes, duck preserves, etc., are considered part of "nature". If the California biting flies are pollutants are the Canadian species a form of "wildlife"?

Dr. Provost indicated yesterday that the percentage of crop losses due to insects has not declined since the introduction of insecticides, and Dr. Rai stated he felt populations of mosquitoes have remained the same over the years in spite of chemical control efforts. I do not know the situation for crop losses, but the statement about mosquitoes is a generalization I cannot agree with. In some areas of California there may be larger populations of mosquitoes today than in former years, but there also has been an increase in the land area irrigated. However, for most areas of the U.S. I believe there are far fewer mosquitoes now than in former years. This has resulted from conscious control efforts and, in part, from urbanization wherein asphalt simply has replaced mosquito breeding sites.

One potential method of control mentioned by Dr. Peterson was the use of traps. In recent years I have been working with CO_2-baited traps which attract and catch tremendous numbers of blood-sucking flies. Such baited traps do have potential for reducing populations of biting flies (Anderson & Hoy 1972), but up to the present they have been used primarily in basic research.

Dr. Peterson's suggestion that we are concerned basically with man-biting flies was too restrictive for me. From my perspective I feel we also need to include in our area of concern a number of biting flies which affect livestock as well as man; this would include the horn fly, *Haematobia irritans*, the stable fly, *Stomoxys calcitrans*, and in all probability, the face fly, *Musca autumnalis*. Two other minor points of controversy I wish to mention before concluding on an agreeable note are: 1) I do not think we have been as naive in judging the severity of biting fly problems as Dr. Laird suggested, and 2) I do not look with alarm at the vectoring of host specific species of *Leucocytozoon* and other Hematozoa to wildlife. In the case of the latter organisms, I feel they are an essential part of an ecosystem in which they function to keep the system in a gently oscillating balance; one might even conclude on a teleological basis that such parasites have survived because they were in some way beneficial to the host species. With respect to the first point, I feel that in most instances the severity of biting fly problems has been first recognized and complained about by the local inhabitants before anything much has been done about the problem. Mosquito abatement districts, for example, generally evolve at the local or grassroots level. However, there are exceptions like vacation and resort areas where temporary visitors can play a significant role in evaluating a biting fly problem. But these generally are located in limited, somewhat unique areas which accounts for their popularity.

In conclusion, I agree with Dr. Laird's suggestion for an interdisciplinary approach to control of vector or noxious species in the future with individuals in many different disciplines directing their efforts toward a primary target organism. I also agree with the implication that future attempts to control these species should be carried out within the context of a broad integrated resource management program. Drs. Hocking and Laird both emphasized the value of education for both future students and the general public, and Dr. Laird noted the limited usefulness of computers for solving ecological problems if future biologists rarely set foot in the field. These points are well taken, but I also would note that, at least in the U.S., with more and more of our present-day students having metropolitan rather than rural backgrounds, the structure of many of our biology and entomology courses is going to have to be modified to the extent of including more field trips, field lectures and field exercises, and perhaps a comprehensive summer field course such as is required at the University of California. This, hopefully, will be one way of insuring that the next generation of biologists will, as Dr. Laird and others hope, contain more observers than does the present generation.

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OPEN DISCUSSION

Fredeen: Would there be any interest in a short discussion of insect pheromones?

Judson: While we usually think of air-borne chemicals as pheromones, there is one very interesting example of a non-air-borne chemical, namely matrone, which I think satisfies the requirement of being a pheromone. Matrone might be of potential usefulness, although as Dr. Rai has said, there would be a number of problems in development. However, I think the potentiality is great enough that matrone should be tested further.

Osgood: During the past 3 years we have been working on an oviposition pheromone of *Culex tarsalis*. It is present on the eggs, contributed by the female, and appears to be a 1,3-diglyceride. This summer Dr. McLintock and I plan a preliminary field trial of this pheromone to determine its effectiveness in the field.

Downes: From what little is known of sex pheromones in biting flies, it appears that at best pheromones are restricted to an extremely short range effect of a few inches only. If one is looking for the possibility of controlling biting flies through the process of assembly of the sexes for mating, then I suggest the process to address one's self to is that of swarm formation. In many species a large fraction of mating takes place in swarms. In all species it would appear that these swarms are determined by definite situations in the environment that can often be mimicked successfully artificially. There is scope for experimentation along the lines of creating swarms artificially and so exterminating the males by the thousands and millions by some very simple mechanical device or other process.

Provost: I would like to follow up on Downes' remarks. Especially if we are to resort to genetic methods of control, it is quite important that we know all the details of insemination in nature by biting flies. In a recent study to determine the time of insemination of *Aedes taeniorhynchus*, we found the females had to be more than 30 hours old before any significant amount of insemination occurred. This was particularly surprising in view of the observations made by Drs. Nielsen and Haeger and myself several years ago that thousands, if not millions, of female *A. taeniorhynchus* mated on the migratory exodus.

Obviously, insemination does not occur in this "mating" at the time of the migratory exodus and most likely takes place in male swarms later. Consequently, I think the point brought out by Downes is significant. If we want to learn more of the exact circumstances of insemination in nature we need to pay more attention to the male swarms.

Anderson: For a number of years I have been working on blood-sucking flies in California that attack deer. I have found that in all cases the females are inseminated before they seek the host. Thus mating always preceded blood feeding in *Culicoides*, culicids, simuliids, tabanids, and ragionids collected feeding on deer or collected in CO_2-baited traps.

Laird: In this entire Symposium to date we've spoken of "control" in the sense of "control of adult female and larval biting flies." We find remarkably little in the mosquito literature, for example, on the control of eggs, pupae and males. I wonder whether we're missing a trick here? All male mosquitoes (and some females, in northern latitudes) feed on plants, whether from flowers or at stomata. The important issue of whether they display specific feeding habits thus arises. There is some evidence that they do, from work undertaken by Professor A. A. Abdel Malek (Cairo University) at Chalk River and at Siwa Oasis on the Libyan Plateau. Does this open up an unexploited pathway to control? Could we hope to consider applying the infective stages of certain microbial control agents to plants that are food sources for male mosquitoes (let alone northern females), so as to bring about morbidity and mortality – perhaps even transmission of pathogens between the sexes? Again, if that proved impracticable, could chemical pesticides or chemosterilants be brought into contact with adult mosquitoes via topical application to food plants? Of course, investigations along these lines would call for fuller baseline information than is yet generally available on such things as whether or not male mosquitoes normally feed before insemination takes place.

Běliček: Many, if not all, biting flies require a specific microorganism, symbionts, to sustain life. This life dependency of insects on their symbionts offers a good mechanism for control of these insects. It may be easier to control insect symbionts and subsequently the insects themselves rather than to control insects directly by other means. Because this area of control was not mentioned, I would like to ask if anyone can inform us about the potential and feasibility of control in this area? Has any research been conducted along these lines?

Poinar: This is a very good point and other than a project concerned with control of *Glossina* by chemically affecting their bacterial endosymbionts, a rather neglected one. It is amazing that this area hasn't been investigated further.

McLintock: We should not forget that, at least if my memory serves me right, only those insects which feed 100 per cent on blood in their entire life cycle have symbionts, while those that have other sources of nutrients, do not.

Bay: In his discussion, Dr. Poinar commented about Dr. Reeves finding a pathogenic bacillus in *Aedes* species. What is significant, I think, is that this bacillus is from *Culex tarsalis*, and is not particularly lethal to the *Culex* group. And so, we go back to traditional parasitology where a parasite in a misplaced host may be more devastating than in its natural host. Perhaps we should be looking more in this direction: picking up parasites in related species where they are in some form of balance with that particular host and trying it in other species of the same genus or family.

Service: One sees the mosquito iridescent virus in the fourth instar because it is iridescent. I presume the virus is present in younger instars, but the viral load is not great enough to cause interference. I would like to ask Dr. Chapman if there is any information on the mortality in the younger instars?

Chapman: If one exposes first instar larvae to MIV particles, a certain number of larvae will become infected, but this infection is not visible. When the larvae reach the third or fourth instar, some will start showing symptoms of the infection. If there are virus particles still in the habitat, some of the third and fourth instars will pick them up, but no signs of infection are apparent and the larvae do not die. The females will pass the virus to the next generation. In a recent paper by Summers and Stoltz where *Aedes taeniorhynchus* larvae were exposed to MIV and then sectioned it was found that degradation of the virus particles was so rapid that not enough virus was available to get into the haemocoel and cause infection.

Anderson: I would like to ask Dr. Chapman if he thinks insect pathogens should be subjected to the same screening criteria as pesticides?

Chapman: I certainly think insect pathogens should be screened. We should know all about the non-target organisms. Another item which should be of concern in this regard is the possible resistance of pathogens and parasites.

Rai: I would like to answer some of the questions posed by the discussants. One question by Dr. Anderson concerned the univoltine mosquitoes in northern Canada and would one have to introduce a genetic factor for several years to get control because there is only one generation a year. As consideration of genetic control of Canadian biting flies is premature at this time, I can't answer this question completely. However, if and when genetic control mechanisms become effective for northern Canada, the number of generations per year won't matter. When a genetic factor is introduced into a population, it remains and will manifest itself in following years as the population builds up in the spring.

Dr. Anderson also asked if an autogenous form could be used to replace an anautogenous one. We have mutations determining autogeny versus anautogeny, so I agree that this is a good possibility for population replacement – replacing either a vector with a non-vector or a pest with a non-pest.

The third question is a significant one. Dr. Anderson asked about the criteria used to determine if trials involving genetic factors were successful. The criterion one uses is some type of population sampling method, e.g., release-recapture, which gives an estimate of total population density. I do not wish to leave the impression that, as of the present time, anything other than the feasibility of genetic control has been demonstrated.

Baldwin: To be effective, large numbers of flies in which a condition such as sterility from a translocation has been induced must be released in wild populations in an attempt at control. How does one produce large numbers of insects by laboratory rearing, when selected lines show significant sterility?

Rai: Yes, indeed, this may be a problem. However, it is precisely because of this difficulty that people are really looking for translocation homozygotes which, in theory at least, should not affect the fertility.

Anderson: Considering that *Aedes aegypti* is an artificial container breeder, wouldn't it be possible to eliminate a high percentage of the population by a good clean-up campaign rather than involving sophisticated approaches? What is WHO's overview in this regard?

Laird: I wish to support Dr. Anderson's remarks questioning the desirability of essentially long-term field studies of highly sophisticated approaches to the control of *Aedes aegypti* in Southeast Asia. Like him, I cannot but feel that as was so clearly demonstrated in the successful campaign against yellow fever in Cuba at the turn of the century, this important disease vector can be controlled on the basis of already-existing knowledge. Purely sanitational measures can be, as they have been in the past, brought to bear on *A. aegypti*'s domestic container-type larval habitats so as to interrupt disease transmission. From personal experience of the region where haemorrhagic dengue is now being spread by *A. aegypti*, I am well aware of the considerable difficulties awaiting sanitation personnel endeavouring to destroy, mosquito-proof or otherwise deal with the production of this mosquito from, artificial containers. But the job, including that part of it associated with the problem of stacked automobile tires of economic importance at the local level, *can* be done. In this instance, to await the development of complex control methodologies with genetic and invertebrate pathology components seems somewhat parallel to awaiting the arrival of a flame-thrower before dealing with a case of shoplifting by a little old lady.

Rai: In Theory I agree that container breeders such as *Aedes aegypti* could be controlled by improved methods of sanitation, but in practice the clearance of the tire dumps would solve only a small part of the problem, and in a city like Delhi it would be an extremely difficult task in itself. Were the solution as simple as has been suggested then the species would probably have become extinct long ago.

However, in some places essentially 100 per cent of the breeding places are water containers inside houses. The reason we selected a tire dump for study was simply because it happened to provide an isolated population suitable for a feasibility study. First of all we wished to collect data on various aspects of field ecology and population dynamics, and then to carry out feasibility studies for genetic control in the same areas. Our objective at this stage has not been to eradicate the mosquitoes from the tire dump, but merely to use this site because it provided the conditions we required.

SUMMARY

Rapporteur . . . . P. S. Corbet

I am first going to review what was said by the speakers this morning, and then refer to what was said by the discussants and discussion leader; then I am going to try to separate out the main points that I think emerged from today's deliberations and that may constitute conclusions and possibly guidelines for action. There will be a little repetition in this, but I hope not too much.

Looking now at the morning papers, the first one was a review of the applicability of biological control principles to medical entomology and the second two were papers on the state of the art and areas of promise, both in the use of pathogens and in genetic manipulation.

Dr. Bay's paper was a thoughtful analysis of biological control as an approach, its strengths and its limitations when applied to medical entomology, and the extent of our present understanding of the reasons for these strengths and limitations. Biological control was defined, we learned what it is and what it is not. Dr. Bay referred to the ladybird fantasy and the great crusade, reminding us that success has its dangers unless we know why that success occurred. He pointed out that, despite the dramatic success of the *Vedalia* introduction, we still do not know how to recognize in advance a successful control agent. It is still more an art than a science. However, we do know some of the attributes that a biological control agent must have if it is to be eligible for success. It is desirable that it be a one-host predator, more like a parasite than a predator; it must also have good searching ability at low host density. Dr. Bay reminded us that natural enemies of mosquitoes, at least those that have so far been identified, are generally not so well suited for purposes of biological control, at least classical biological control. They are not completely reliant on their host, and they are not host-specific. He then gave us a brief review of some highlights of the history of biological control in medical entomology. Comparing agricultural insects with insects of medical importance against the background of biological control, he pointed out that few agricultural insects become pests in the presence of natural enemies and without man's interference, but most biting flies are pests in the *absence* of man's activities and in the *presence* of their natural enemies, particularly in Canada. Dr. Bay gave us a few examples of successful biological control programs involving medically important insects. Looking in detail at some of the agents which have been observed feeding on mosquitoes and other biting flies, he warned us that it is one thing to record the existence of a parasite or predator; it is quite another to have identified a regulatory factor. Predators and parasites of biting flies appear to result in substitutive mortality rather than additive mortality, and it is additive mortality which is needed in biological control. Some of the advantages of biting flies as candidates for biological control are that the control can be applied during the life cycle because it is the adult that causes the nuisance or damage. A disadvantage is our great difficulty in coming to terms with pest tolerance levels, particularly in the case of biting flies, the vectors of disease, because in this case, almost a single fly can be too many. Despite some of these difficulties that Dr. Bay identified, he saw biological control of biting flies as a viable area that we should continue to pursue. It will not have the impact efficiency or convenience of chemical pesticides, with the possible exception of certain pathogens which he considered approached these chemicals in promise. He concluded by showing us illustrations of some particularly striking, but less familiar, predators of mosquito larvae and reminded us once again of the distinction between a predator and a regulator.

In the second paper, Dr. Chapman reviewed known agents reported from biting flies in four groups, and he gave his opinion of the promise that each group holds for a control method. In his introductory remarks he pointed out that out of the 150 or more pathogens and parasites that have been reported, only five so far have had field releases. This reflects the fact that only a few reach the stage in which they can be disseminated, and all these are mosquito pathogens. It also reflects our past reliance on pesticides and the correlated lack of support for basic studies needed to develop alternative methods. This situation has improved somewhat in the last two decades but it is now deteriorating again. In the case of Protozoa, the first of the four groups that he told us about, he stated that almost half the Canadian mosquitoes have been reported as host of microsporidia but that only three species of microsporidia could be maintained or transmitted in the laboratory. In the case of fungi, *Coelomomyces* looks promising in mosquitoes; it persists in ponds and it sometimes shows high natural infection levels. An obstacle which is shared by the protozoan parasites is that they are not easily produced in large amounts of inoculant in the laboratory and so cannot easily be disseminated. Viruses of biting flies have only been known since about 1963 and the best at the moment seems to be a nuclear polyhedrosis virus of mosquitoes. Research in viruses is still in its infancy.

The fourth group he told us about were the Nematoda, particularly the mermithids. These show excellent promise in blackflies and perhaps even greater potential in mosquitoes. The most promising agent at the moment appears to be *Reesimermis nielseni*, which after almost six years of intensive study can now be cultured *in vivo* in very large numbers and disseminated in the field. The existing methods pioneered in Dr. Chapman's laboratory can produce enough inoculant weekly to treat 600 acres. In summary, Dr. Chapman said that too few agents have reached the stage when their potential can be tested. We need funds and people, and concerted effort on problems that have been identified as having high priority.

In the last paper this morning Dr. Rai told us about the progress of work in genetic control and the prospects of this method. He gave us a progress report and an explanation of the most promising techniques available for genetic manipulation. He considered this approach worth examination, in part because resistance was not likely to be a problem, and because it is very gentle in its environmental effects. Progress so far in this area has been mainly theoretical but the results of feasibility trials are encouraging. A point that he made earlier on is that in order to get the necessary background knowledge for a feasibility trial in genetic manipulation, it is essential that the target species can be colonized. So far this has meant that only mosquitoes are eligible for this kind of approach. He said that genetical manipulation offers eight potentially useful mechanisms at this time and perhaps more. Five of these are types of sterility and in addition there is cytoplasmic incompatibility, distortion of the sex ratio, and the manipulation of genes for vectorial capacity. He listed field trials undertaken in the past and now in progress and reviewed and explained current trials in detail. In particular, he told us about the technique which involves the use of translocations and pointed out that this immediately results in fifty per cent sterility, but it also has the effect that it continues to pump translocations into the next generation of the population. He listed species in which translocations are now under study and he listed different kinds of translocations. He showed us also how simulation models, with the use of a computer, can indicate strategies and also allow us to review our assumptions. He stressed that genetic control must be used with insecticides, that is, in an integrated control program. He summarized by expressing his opinion that genetic manipulation has shown great promise in feasibility trials. He does not know yet whether it will be satisfactory for widely distributed populations, and thus it may be premature for Canadian biting flies, although theoretically (and this came up again in the discussion) it seems extremely well suited to a problem of these dimensions.

Moving now to the discussion, I will pick out only a few points and hope that the rest will be covered in principle or in detail in my final summarizing statement.

Dr. Peterson reviewed the taxonomic status of the biting fly fauna in Canada for us. He also listed some of the parasites of biting flies which had not been dealt with in the earlier reviews.

Dr. Poinar mentioned a number of predators and parasites that have not been mentioned previously and in particular drew our attention to a bacterium, *Bacillus thuringiensis* Serotype I which is infective to species of *Aedes* and which can now be grown on an artificial medium. International Minerals and Chemicals are propagating this and testing it now and he asked us to remember that they might make this material available to interested people who wanted to undertake tests in the field. Among other things, Dr. Poinar stressed the distinction between inoculation and inundation as biological control approaches and pointed out that if we are talking about inundation which involves mass propagation and release, the indigenous agents that are now living with the target species are eligible for study.

Dr. Laird pointed out that we should not speak of or think of separate types of control as independent panaceas but we should think of them more realistically as components of an integrated control program – the kind of program that will be needed in future– one that is based on thorough knowledge of relevant facets of biology. At the same time he expressed concern that such integrated control should not be prohibitively expensive and with this he had suggestions for more appropriate allocation of funds. A second point among his remarks that I would mention now is that Dr. Laird saw the need in the future and against the perspective of such programs, for scientists who were not only narrow specialists but competent naturalists, capable of interpreting and synthesizing ecological information. He also gave it as his opinion that microbial agents offer one of the best hopes for the future and he saw it as a vital need that we solve the mass production problems, so that industry can adopt the manufacture of these and make them available commercially to users with instructions for use.

In the general discussion that followed, a few points came out which had not previously been dealt with. On several occasions, speakers emphasized the need for sound background biological knowledge on which to base our control strategies, our conceptions of control and feasibility trials. Other approaches which were mentioned at this time and that we should keep in mind were the use of pheromones, the exploitation or manipulation of swarming, the substance known as 'matrone' which is transmitted with the seminal fluid of the male, and the exploitation of the fact that both sexes of mosquitoes feed on plants or at plants. The possibility of manipulating the symbionts, the micro-organisms that are symbionts in biting flies, was also raised as a possibility.

And now I want to attempt to summarize the main points which I feel have come out of today's deliberations. I am going to offer these in a broad classification under four heads, (1) basic points which underlie the whole subject we are talking about, (2) general points which relate to biological control, the subject of today's meetings, (3) our needs and the obstacles to progress which in some ways are the same thing, and fourthly and finally, (4) a tentative recommendation for action.

Basic Points

1. We must beware of putting the cart before the horse. We need to know the questions before we try to find the answers. As Dr. Peterson says, we have a tendency to expect instant answers before we have enough information to formulate the questions.

2. If we are going to talk about success, we need to have clearly in our minds the criteria for success and this means also the criterion of the nuisance we are trying to mitigate or remove. We often lack such criteria, even though we carry out our tests and this means we must also know the objectives of the tests we undertake.

3. We need to have protocols that will enable us to study the side effects on man and other non-target organisms of the agents we use.

4. Only in this way, by having a clear idea of our objectives, the criteria by which we measure success or failure, and a flow chart for action in our feasibility trials, can we adopt a rational approach towards the resolution of the dilemma of reconciling environmental quality with man's comfort and health.

General Points

1. The distinction has been made between classical biological control (we may call that inoculation) and mass propagation and release (we may call that inundation), and most of the methods we have identified today as having the greatest promise are in the latter category. They fall under the head of mass propagation and release – or inundation.

2. Biological control methods are not self-sufficient but they should be seen as components, as one type of several chemical and non-chemical methods that can contribute to an integrated control program in the future.

3. When identifying agents of promise, in the case of inoculative or classical biological control, we need to distinguish between an agent which is seen to eat a target species and one which is a real regulatory factor. And, for inundative biological control, we need to distinguish between the behaviour of potential agents that can be observed in the laboratory and their real performance in the field.

4. It was agreed that certain areas of biological control hold great promise, notably genetic manipulation and the dissemination of pathogens and especially mermithids.

5. Such methods that we have been speaking of are more sophisticated, difficult and expensive in respect of the foundation knowledge that has to be obtained and the way in which it is applied than are conventional methods involving synthetic, organic, chemical pesticides. Thus they demand a realistic level of support whose continuity can be relied upon.

Needs for Progress and Obstacles to Progress

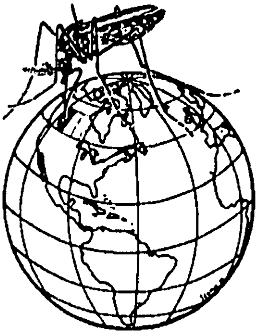
1. First of all, we need methods of colonization *in vivo* and *in vitro*, and effective dissemination techniques in order that we can control the production of agents we are using, and for the genetic studies that are a prerequisite for genetic manipulation.

2. A second need is for more background knowledge, especially in the area of a few key problems in the most promising areas.

3. The third need is that of communicating to the appropriate authorities the nature and dimensions of the needs of this area of research.

Finally, I have tried to bring together these thoughts in a recommendation for action with the emphasis on the practical situation and our immediate needs. In the present financial climate in which the support that we can expect for this kind of work falls far short of the needs we have identified, the best policy may be to focus our attention and available resources on the few methods that hold the greatest promise and lie closest to application, the reasoning behind this being that nothing is so likely to generate more support now as one or two compelling successes. By success is meant something that can be applied on a sound economic basis, not only to vindicate a principle, essential though that is, not only to reduce population levels, essential though that is, but specifically to reduce the frequency of bites or whatever criterion it is that defines the nuisance we wish to relieve.

PROTECTION OF INDIVIDUALS



PERSONAL-USE REPELLENTS AND REPELLENT-TREATED NETTING: A REVIEW OF THEIR EFFECTIVENESS AND RELATED APPLIED AND BASIC RESEARCH

Donald E. Weidhaas

Entomology Research Division
Agricultural Research Service
U.S. Department of Agriculture
Gainesville, Florida 32601

Throughout the world many species of biting flies cause annoyance and spread human and animal diseases. Among the biting flies that we might emphasize while considering personal protection measures are mosquitoes, sand flies, black flies, gnats, tabanids, and stable flies. These insects are represented by many species in many parts of the world and in certain areas occur in extremely large numbers. The most ideal solution to the problem of annoyance and disease would be programs designed to control and suppress these insects to non-injurious, low density or non-vector levels. However, in spite of all the progress made in insect control and drug therapy, the management and reduction of these populations is not possible in many areas for a variety of reasons. These insects have a tendency to occur, breed and fly over large and diverse areas of uninhabited as well as inhabited land. The task of managing and treating large areas for controlling these insects is, in many instances, uneconomical and may be undesirable from the environmental point of view. Source reduction, management, insecticidal methods and prophylactic drugs may protect people in limited areas where population density is high. However, outside these areas, the currently available control and management techniques, though they might be effective, are not practical or economical.

Thus, there are many areas throughout the world, in both developed and developing nations, where the use of protective clothing and repellents is the only means available to individuals for personal protection against the annoyance and diseases associated with biting flies short of leaving the area or remaining in screened or air-conditioned enclosures. This problem can exist in one's own living area; on nature walks; in wilderness areas; while hunting, fishing or camping; while at work, play, leisure or asleep; or while armed forces personnel carry out their assigned tasks anywhere in the world.

Before World War II, certain materials such as pyrethrum, sulfur, oils of citronella, eucalyptus, pine, lemon, pennyroyal, and tansy were used as repellents for insects. During World War II and the following 10 years, many thousands of chemicals were screened for repellency against blood-sucking insects. Many of them showed repellent activity. However, not all of them met the criteria for an acceptable repellent which included: (1) effective protection of a treated area for several hours with all types of subjects and under all types of conditions, (2) resistance to loss of activity by water, sweating and abrasion, (3) complete freedom from irritation and toxicity when used repeatedly on human skin or clothing, (4) cosmetic acceptability, (5) cheapness and (6) availability.

During and after World War II, many effective repellents were developed. These included such materials as deet (the approved common name for *N,N*-diethyl-*m*-toluamide), ethyl hexanediol, dimethyl phthalate, dimethyl carbate and Indalone® (butyl 3,4-dihydro-2,2-dimethyl-4-oxo-2*H*-pyran-6-carboxylate) and others for use on skin or clothing. Butyl ethyl propandiol, undecylenic acid, *N*-propylacetanilide and benzyl benzoate were developed for use on clothing. Each of the chemicals may be better for a given type of treatment against a certain species of insect or with different people. Deet has proved to be the most outstanding all purpose individual repellent yet developed.

All of the repellents approved for application to skin have disadvantages and are not entirely satisfactory to those who use them. They are not effective for long enough periods of time and are subject to loss by abrasion, evaporation, absorption and immersion in water. They may feel oily on the skin and affect paints, varnishes and plastics. All cause a stinging sensation on the eyelids and lips. Repellents are effective only when present on the skin or clothing in relatively large quantities. Although the amount varies with the individual, the chemical, the insect species and other conditions, the minimum effective dose ranges from about 0.05 mg/cm^2 for deet to more than 1 mg/cm^2 with dimethyl phthalate on arms exposed to avid *Aedes aegypti* (L.) in laboratory tests.

Programs on the search for and development of better repellents have been maintained by various research groups. The Army Medical Research and Development Command has supported a continuing program on repellent research. Research on repellents has fallen into several general categories. The screening of unknown chemicals for repellent activity followed by the evaluation of promising chemicals for biological effectiveness and safety has been a continuing program both at our laboratory and in other groups. We have been fortunate to have the competence of toxicologists of the Army Environmental Health Agency in determining the safety of chemicals for application to humans for biological testing of promising chemicals. Factors affecting the protection time obtained with standard repellents have been thoroughly investigated. Formulations that were designed to extend the protection time or enhance the cosmetic acceptability of known repellents were investigated in detail and new formulations continue to be made and tested. More emphasis has been placed on studying factors involved in the attraction of mosquitoes to human hosts with the hope of finding new approaches to repelling blood-sucking insects. Basic studies on receptors and receptor systems in insects and the mode of action of repellents and attractants on insects have been initiated. Research has been undertaken on the study of spatial repellency and the application of repellents to netting for use as jackets, bed nets and head nets. Finally, a search for systemic repellents was undertaken.

In spite of all these approaches to the problem, significantly more effective or longer lasting repellents or formulations have not been forthcoming since the introduction of deet. It is hoped that research will be able to develop more effective materials or new approaches to the repellent problem. For this presentation, I would like to review, in general, aspects related to the development and use of insect repellents covering such items as mentioned previously. Also I will review some of the more recent research. Primarily in the interest of time, but also in acknowledgment of my own limitations, I have decided to limit my discussion to research conducted at our laboratory. There are many in the audience with an interest and competence in this general area of research and other research can be presented and reviewed in the discussion period.

Systemic Repellents

The development of a material that could be administered orally and protect against blood-feeding arthropods has been a dream of many scientists for years. At one time our laboratory initiated a screening program to evaluate compounds as possible systemic repellents. Compounds were administered by stomach tube to guinea pigs at various doses and mosquitoes, fleas and lice were placed on the guinea pigs to see if feeding was inhibited or if toxicity was encountered. The search for systemic repellent compounds was unsuccessful, and the screening was discontinued. The problem is partly related to the fact that currently known repellents have to be applied in large amounts. There seems to be little hope of being able to attain the amounts required with available repellents via systemic action. The development of a systemic repellent will require finding a mechanism with a completely different mode of action.

Screening for Repellent Activity

At various locations in the United States, efforts are continuing to find and screen new compounds for repellent activity. We continue to screen materials sent to us from different sources. Recently, through the help of the Army Medical Research and Development Command, the Armed Forces Pest Control Board and the Walter Reed Army Institute of Research, we have been provided a source of several thousand chemicals to be tested as candidate repellents. These compounds are screened rapidly, and those with activity are compared to deet and dimethyl phthalate for protection time and minimum effective dose. We hope to find new types or structures of chemicals with repellent activity. Although some compounds have been found that are more effective than deet in length of protection time and minimum effective dose, new type structures with repellent activity have not been found. Studies on toxicology of effective compounds must be completed before further testing for repellent activity can be conducted.

I will not take the time to review our screening methods in detail since these have been summarized by Smith (1970). This topic can be considered in the discussion. We might comment that the methods used to screen and evaluate repellents in general include, in our order of preference, tests with human hosts, animal hosts, inanimate attractants and no attractants at all. We, at our laboratory, feel that screening procedures should be related as closely as possible to the final way in which a repellent is to be used, i.e., against a human host. As Smith (1970) pointed out: "Modern scientific evaluation of repellents may be said to have begun with Granett (1940, 1944), who used the relative length of protection of competitive repellents as his criterion when he tested compounds on the human skin at standardized conditions. Granett's methods, with some modifications, have been used in most subsequent testing programs, and in combination with tests for resistance to rinsing and rubbing or wiping, provide the ultimate comparison on which selection must be based."

Formulations

Over the years, a considerable amount of time and effort has been expended in evaluating various mixtures and formulations in an attempt to increase the protection time and cosmetic acceptability of insect repellents. In an unpublished SPECIAL REPORT (71-01G) of our Gainesville laboratory (Evaluation of Repellent Mixtures Against Three Species of Mosquitoes and Stable Flies, 1971), Gilbert summarized cooperative studies on over 2,000 formulations prepared by the Smith Kline and French Laboratories. This comprehensive study, though done quite some time ago, has not been available and should be of interest to other researchers. Little success has been obtained to date in extending the effectiveness of repellents through various formulations with the exception of formulations containing zinc oxide.

Factors Affecting Protection Time Obtained with Repellents

Several articles by Smith (1966, 1970) and Smith *et al.* (1963) have summarized the studies at our laboratory on factors affecting the protection time obtained with repellents. It would be of interest to summarize their conclusions based on studies with 3 well-known repellents – deet, ethyl hexanediol, and dimethyl phthalate – and mosquitoes and human subjects. They point out that it is not correct to assume that mosquitoes will be repelled as long as any repellent remains on the skin. Repellents must be present on the skin in relatively large amounts and a minimum effective dose (MED) has been determined for all three repellents against *A. aegypti*. This MED did not differ greatly with different men and women, but varied considerably with the 3 repellents studied.

It was not possible to obtain a correlation between the natural attractiveness of the human host and the protection time afforded by repellents, i.e., the most attractive subject did not obtain the shortest protection time or vice versa. Furthermore, evidence was obtained that these repellents did not deteriorate on the skin or lose effectiveness by admixture with sweat, carbon dioxide, or water. Other studies have indicated that repellents did not affect the evolution of moisture or lactic acid from the arms of human subjects and reduced the carbon dioxide output with only some subjects.

Thus, to date, loss in protection afforded by repellents appears to be correlated with its rate of loss from skin rather than differences in attractiveness of individual hosts or changes in the attractive factors associated with hosts. This loss can occur by abrasion, evaporation and absorption. Loss by abrasion is the most important factor in the practical use of repellents, but the most variable since it depends upon rubbing. Evaporation rates of repellents were about the same for men and women for a given repellent, but there were more pronounced differences in absorption rates with individuals. The differences in absorption rates accounted for most of the individual differences in total rates of loss observed.

The available information indicated that the natural attractiveness of hosts, chemical degradation of repellent, or admixture of repellent with human emanations could not be correlated with protection time obtained with repellents, and that protection time was related to rate of loss of repellents. When the amount of repellent present on the skin was made to be less than the minimum effective dose by any of a variety of methods, protection from biting was no longer assured.

Attraction to Human Hosts and Basic Studies

One hope of many researchers is that basic studies on the attraction of mosquitoes to human hosts and their feeding behavior as well as studies on the receptor systems involved will lead to new methods of repelling blood feeding insects. Since I mentioned that I planned to limit my presentation to results obtained in our laboratory, this area would be a fertile field to explore in the discussion period with the interested individuals involved.

I would like to mention only studies with lactic acid at our laboratory in olfactometers and in the field. Acree *et al.* (1968) reported that L-lactic acid was the major component attractive to female *A. aegypti* found in human emanations they examined. The fact that they also reported in this paper that the presence of CO_2 in addition to that already present in purified or filtered air was essential to elicit the attractive response seems to have been largely overlooked. Smith *et al.* (1970) reported on a series of comprehensive tests on L-lactic acid as an attractant for *A. aegypti*. Without going into detail on much of this research, I would like to simply follow this point of the concurrent need of carbon dioxide with lactic acid to elicit attractive response in *A. aegypti*. As stated by Smith *et al.* (1970): "Vapors from authentic L(+)-lactic acid released from glass sample tubes at rates comparable to those released from hands were attractive either in combination with carbon dioxide in filtered air, or alone in room air. However, the synergistic effect of CO_2 on the response to lactic acid did not persist more than a few seconds after the mosquitoes left an atmosphere rich in CO_2." Since carbon dioxide in the past has been referred to as an activator, a synergist and an attractant in mosquito response, this requirement for both lactic acid and carbon dioxide (or components present in room air) for attractive response in olfactometers is interesting. The studies described thus far were conducted in dual port olfactometers. Additional studies involved the use of a black, rectangular box, or wind tunnel, divided into 11 compartments. Practically all avid *A. aegypti* females tested flew the entire length of the tunnel when lactic acid and carbon dioxide were introduced upwind at its far end; half the distance up the tunnel when lactic acid and carbon dioxide were introduced at the midpoint of the tunnel, and half the distance up the tunnel when either of the 2 components was introduced at the far end and the other at the midpoint of the tunnel. In other words, female *A. aegypti* tended to follow the air stream only when both components were present simultaneously in concentrations above normal background or threshold. It is interesting to note also that our attempts to increase attraction of mosquitoes to carbon dioxide traps in field studies by the addition of lactic acid have been unsuccessful – a result that is difficult to explain in view of the data obtained in olfactometers. Either there is a difference in response to different attractants by different species of mosquitoes, the lactic acid was not presented properly, or the presence of lactic acid or other chemical attractants in the environments precludes the need for additional amounts. Attraction to human hosts appears to be a complex of many factors.

Repellents Applied to Netting

Another approach to the problem of better repellents has been the concept of the development of "space repellents". Gouck *et al.* (1967) described the goal of finding repellents that might be applied to limited areas such as a collar, hat or visor to protect the face or neck. Other investigators have had similar ideas. Schreck *et al.* (1970) reported on a special study of the spatial repellency of 44 repellent molecules. All of the materials except 1 significantly reduced the approach of mosquitoes to treated hands tested in the dual port olfactometer. Sixteen compounds were highly effective in reducing approach. They concluded that repellents may initially reduce annoyance by spatial activity, but complete protection from biting depends on both spatial and contact repellency.

Although the goal of developing highly effective uses of repellents based only on spatial repellency has not been achieved, the use of repellents applied to wide mesh netting now seems to offer much promise in uses as bed nets, jackets and coverings for openings in enclosures. Gouck *et al.* (1967) tested a large number of compounds for their effectiveness and have conducted field trials with the treated netting (Gouck *et al.* 1967, 1971). An example of the utility of this type of netting can be cited from Gouck and Moussa (1969). Bed nets made of 4-mesh-per-inch pressed cotton netting and treated at a rate of 0.5 g of deet or M-1960 (a mixture of 30 percent benzyl benzoate, 30 percent *N*-butylacetanilide, 30 percent 2 butyl-1,3-propanediol and 10 percent emulsifier) per 1 g of netting provided complete protection against *Culex pipiens quinquefasciatus* Say and *A. aegypti* for 15-17 weeks.

Our basic needs in improving the effectiveness or protection time obtained with repellents seem to fall in several different areas including: (1) screening of compounds to find repellents of different chemical groupings that may be more repellent or longer lasting and may have a different mode of action than that of currently known repellents; (2) further concepts on extending the length of time that repellents are effective on treated surfaces (One such example of this is the work in progress at the University of Tennessee attempting to unite repellent moieties to skin anchoring compounds. The idea being that the repellent could be released through hydrolysis while the anchoring compound would slow down the rate of loss of the repellent.); and (3) finally, basic research on the mode of action of repellents and attraction to human hosts in an attempt to find new means of protecting individuals from blood-feeding arthropods.

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NOTE. This paper reflects the results of research only. Mention of a pesticide in this paper does not constitute a recommendation of this product by the U.S. Department of Agriculture.

BITING FLIES: THE NECESSITY FOR A NEW SYSTEMATICS

J. A. Downes
Entomology Research Institute
Canada Department of Agriculture
Ottawa, Ontario

There has been much discussion recently of the need for specificity in methods of insect control so that unintended effects, perhaps harmful, will be minimized. Equally, I think, we must recognise to the full the specificity and diversity in the insects themselves, lest again action should be misdirected.

It seems to me that insect systematics as commonly practiced does not adequately come to grips with the complexity and diversity of the organisms it studies – certainly not in the case of the biting flies. It thus fails to make contact with many of the themes that concern other biologists, and its analyses often do not extend to the populations that exist in real life, with which they have to deal.

To a great extent and even, perhaps, increasingly at the present day, systematics is directed to identification. The description is a relatively brief account of certain predominantly external features selected mainly with a view to distinguishing the insect in question from similar forms. It can thus be used with relatively little prior knowledge; or it can be used by a machine. Machines, now or in the foreseeable future, can scan an insect in a variety of ways, construct keys, and process the specimen whose name is required. The usefulness of all this is evident, and it seems likely that the initial inspection and description will in future be directed more and more towards machine methods.

It must be noted however that the characters used are selected primarily for their clarity and value in a process of identification. Typically they are not characters of importance in the bionomics or structure or physiology or phylogeny of the insect in question. Thus the systematist is not fulfilling what to me is one of his main functions: to assemble and set out what is known about the insects he is dealing with, and by making comparisons and classifications to bring order into this information so that it can be used as a foundation or background or source of interpretation in further studies. To give a familiar and frustrating example: while the female of mosquitoes, and of many other biting flies, is usually described by a fair range of external features, the male is represented by the terminalia only, which suffice for identification! This curious practice is found in both the current handbooks of North American mosquitoes and in many of the regional monographs; and if, in the course of behavioural studies, for instance, one wishes to obtain some comparative information on the antennae or legs of the male, it is nowhere to be found in the systematic literature later than the classic work of Howard, Dyar and Knab (1913-17). Most biting flies, it may be noted, exhibit a sexual dimorphism that extends to virtually all structures and organs used in taxonomic descriptions (antennae, eyes, mouthparts, head sclerites, wings and wing venation, legs, claws, terminalia, colour pattern, chaetotaxy, general body proportions, distribution of sensilla), and it is impossible, except quite approximately, to infer the character of one sex from a description of the other.

A further consequence is that the systematic accounts, precisely because they do not take note of the totality of features, are in fact often very inadequate; the classifications and identifications arrived at do not reach far enough for practical purposes, they do not reach to the natural units that really exist and play a distinctive and independent part in the ecosystem. This is my main theme in this paper. I do not challenge the usefulness of the standard taxonomic identification as a first step in a process; but it is now being shown repeatedly that it is only a first step.

How Many Species? A. Cytological studies on black flies

The recent history of the systematics of North American black flies is especially interesting. In terms of 'species' of the usually accepted type, the description of the North American fauna of Simuliidae is approaching completion; perhaps two-thirds or more have been described and named. But is this the whole story?

Rothfels and his collaborators (1953 to date) have made a long series of investigations on the structure of the chromosomes of many species of black flies. The chromosomes of the salivary glands of the full-grown larva are of the giant polytene type, and show a succession of transverse bands that reflect the genetic structure. They are relatively easy to inspect in great detail and the homologous members are closely paired, typically for the whole of their length.

A particular segment within a chromosome may sometimes become inverted. The inversion is recognised by a reversal of the order of the pattern of banding and often also by a local failure of pairing. The limits of the inversion can be determined very precisely because of the complexity of the banding, and a particular inversion can thus be recognized with great assurance. For a similar reason, a particular inversion is very unlikely to be formed again, with exactly the same limits at each end, by chance. Thus the banding pattern of the chromosomes provides a great series of structural characters of special value, more sensitive than many ordinary characters of chaetotaxy or shape of appendages because they are very precisely defined and less likely to be duplicated by convergence.

Many black fly populations carry one or more such chromosomal inversions at various frequencies, and the inversions occur in the homozygous and heterozygous conditions in the expected proportions. Evidently, like many other mutations, these floating inversions are associated with only small developmental effects, not interfering with interfertility. Other inversions, however, characterize all individuals of a taxonomic species; and in fact most of the species investigated differ by one or several of these chromosomal changes.

The earliest studies showed that in the black fly identified as *Prosimulium hirtipes*, these chromosomal differences existed sympatrically without the appearance of heterozygotes; '*hirtipes*' that is to say, consisted of a number of species, which did not interbreed (Rothfels 1956). In several cases structural differences distinguishing the forms were soon discovered (e.g. Syme and Davies 1958) and chromosomal, anatomical, and life history studies have proceeded hand in hand. At the present time '*hirtipes*' in North America consists of more than a dozen species arranged in two species groups, and distinguishable both chromosomally and by structural details of the larval, pupal and adult stages. 'True *hirtipes*' was recognized as restricted to the palaearctic, and is now known to consist of yet a third considerable species group (Basrur 1959; Rothfels and Basrur 1960; Basrur 1962; Ottonen 1966).

Several other apparent species have been examined in the same way. *Eusimulium aureum*, originally considered a holarctic species with a wide distribution in North America and Europe has been shown to consist of seven cytological forms, probably all true species. Two occur sympatrically in Ontario, two more in the prairies, a single species in California and two more in Europe (sympatric at least around Leningrad) (Dunbar 1959). *Simulium tuberosum* in southern Ontario consists of at least four breeding units, all sympatric; but they are very closely related and it is possible that hybridization sometimes takes place since they have certain 'floating' inversions in common (Landau 1962). In the *Eusimulium congareenarum* group, on the other hand, the cytological study served mainly to associate and define a group of already described closely related species, and only two new species were discovered in the process (Dunbar 1967). Recent work on the western species *Prosimulium onychodactylum* has revealed the largest group of siblings yet discovered, no less than 12 in all, the majority of them sympatric in streams around Mt. Hood, Oregon. On the other hand, *Simulium vittatum*, a species that is very variable both in appearance and ecologically, proves equally to be a single highly variable entity when examined cytologically; almost all the many inversions recognized appear in the heterozygous condition in the proportions expected from random matings (Pasternak 1964).

Dunbar (1969) has also shown that the important African black fly *Simulium damnosum* consists of at least nine segregates, and the studies are still continuing. The existence of several entities within this 'species' had already been suspected on ecological grounds, but there was no indication that it was composed of such a large group of independent forms, nor had any of the forms been clearly delimited.

Overall, it may be predicted that the numbers of species of black flies existing in Canada (or North America, or elsewhere) is not merely slightly greater than the number now recognized, but more like five times as great.

There is no reason to suppose that these results are peculiar to black flies. The genus *Chironomus* is undergoing a similar 'explosive speciation' at the hands of cytologists, and chromosome banding studies are playing an increasing role also in *Anopheles* and other mosquitoes.

The study of the polytene chromosomes in black flies is making important or decisive contributions also to other discussions central to modern systematics. A remarkable feature of most of the groups of newly recognized siblings is that the members have a strong tendency to be sympatric and often occur together in the same stream, even in the same samples. The orthodox position of modern systematics is of course that sympatric speciation does not take place; the process of building up reproductive imcompatibility demands, as a substrate, some degree of spatial separation. There is no direct proof that these flocks of sibling species have in fact been generated sympatrically, but the phenomenon of their sympatric occurrence is sufficiently common and extensive to suggest this very strongly. The possibility arises that the process of speciation depends upon an incompatibility brought about as a result of the chromosomal changes (Dunbar 1965; see also White 1969) rather than in adaptive behavioural or structural changes developed in isolation. It seems urgently necessary that systematists should study the bionomics of these sympatric siblings and determine whether they are maintained by differences in behaviour or ecological preferences, or by gametic incompatibility or early death of the hybrids.

The inversion systems in the polytene chromosomes of black flies enable the relationships between a group of species–the members of a subgenus or genus for example–to be determined with precision, and an unequivocal phylogenetic diagram constructed. The process is, in essence, a very simple one. A derived form differs from its progenitor by, say, a single specific inversion. A further derived form differs from its immediate ancestor by yet another inversion, that overlaps, and thus includes a part of, the first. A part of the first inversion will thus be displaced to a new position in the chromosome, with its banding pattern re-inverted and thus in the same direction as in the original (standard) chromosome. The final arrangement can be derived from the standard only by passing through the intermediate stage; the relationship of the three forms is known with certainty. The method does not, by itself, indicate in which direction evolution has proceeded; it states only the pattern of the relationship, and the starting point (the ancestral form) must be determined from other considerations. A chart of this nature may be seen in Rothfels and Freeman (1966), and a much more detailed version that includes most of the known species of *Prosimulium, Twinnia*, and *Gymnopais* is in preparation (Rothfels, personal communication).

No other method allows the relationship between species and genera to be reconstructed with any comparable degree of precision and certainty.

In many Diptera the chromosomes of the larval salivary glands do not develop the polytene condition, but similar banded chromosomes have been recognized in several other types of highly active cells, including those of the malpighian tubules, the nutritive cells of the egg follicles, and the trichogen and pulvillus cells of the pupa during the secretion of the adult cuticle.

It is surprising that this powerful method, able in many cases to give a decisive answer to the question whether two similar forms are reproductively isolated, and to describe with precision the pattern of evolution of a complex of species, is not being widely exploited in systematic studies.

B. Genetical studies on mosquitoes

Black flies, though well suited to cytological analysis, are difficult to maintain in captivity and no experimental study of black fly genetics has been attempted. In mosquitoes, on the other hand, direct genetical analysis by experimental matings is often possible and a considerable body of information is available. It has been found that a number of well-known species are in fact complexes of closely related forms, in some cases fully isolated sibling or cryptic species and in others forms with various kinds and degrees of genetic incompatibility yet still retaining a certain potentiality for gene exchange. Often there are corresponding ethological differences and sometimes, but not always, small structural distinctions have been detected and have provided the basis of taxonomic descriptions.

The classical case is that of *Anopheles maculipennis* in Europe. Within this supposed species puzzling differences of host range, biting and mating habits and preferred microhabitat were observed, and it was eventually shown that these corresponded to fully or partially reproductively isolated groups within the complex. They were then distinguished visually by hitherto overlooked details in the chorionic pattern of the eggs and the arrangement of coloured scales on the wings. Seven forms maintaining themselves as distinct entities in nature are now recognized; they are sufficiently closely related so that after laboratory matings the eggs begin to develop, but the hybrids either die before hatching, or before emergence from the pupa, or the emerging adults are sterile, or, in three cases, partially or fully fertile females (but no fertile males) are obtained and backcrosses to either parent species are possible (see Marston Bates, 1949). Like the black flies, *Anopheles* larvae have polytene salivary gland chromosomes and the pattern of phylogenetic relationships between these forms is being established. The *Anopheles maculipennis* group exists also in North America, but the species are more distinct from one another both structurally and chromosomally, and probably older (Kitzmiller *et al.* 1967) and in contrast to the European forms they were already recognized as distinct, on normal taxonomic features, before experimental studies were undertaken.

Culex pipiens is a widely distributed species that consists of three subspecies (*pipiens, fatigans* and *australicus*) of the familiar geographic type, differing very slightly in details of structure and more notably in their adaptation to temperate or to tropical life-zones. Cutting across the subspecific distinctions, but studied mainly in western European *pipiens*, there exists on a much smaller geographic scale (e.g. within Germany) a series of more or less incompatible breeding types not distinguishable by structural differences (Laven 1967). The incompatibility is believed to be due to a series of factors that arise between the sperm and the cytoplasm of the egg, rather than to genic differences of the usual type; and the result of a given cross may differ according to the direction in which it is made. Some inter-strain matings are fertile in both directions, others in one only, and others may fail whichever way the cross is made. In the latter case, of course, the two strains (within the same sub-species, and structurally inseparable!) are able to function as biologically (and practically) distinct species. A total of 17 such reproductively differentiated forms have been identified to date.

Anopheles gambiae consists of five readily distinguishable cytological and ecological species, two of which have also been distinguished taxonomically. They occur sympatrically in various combinations. In laboratory crosses the female offspring are fertile but the males invariably sterile and with more or less malformed testes. It is supposed that in nature this partial interfertility is restricted by behavioural differences, perhaps related to mating, and natural hybrids have rarely been encountered. In some crosses the females are reduced below the normal 1:1 ratio or are missing altogether, apparently due to death in the early stages of development. In some crosses also, the males, while sterile, show a hybrid vigour that allows them to compete for mates more than successfully with the males of the parent form. Such crosses therefore would seem to provide possible material for an interesting form of genetic control, which sometimes might even go along with normal insecticidal control since insecticide-resistant strains are known and the release could be made with resistant males (Davidson *et al.* 1967).

It is interesting that these striking cases relate to some of the best known of all mosquitoes. It suggests that the more they are looked for, the more such cryptic and partial species will be found, and that we have as yet only a very fragmentary knowledge of the mosquito taxa of the real world. Gillett, in his new book "Mosquitoes", appears to share this view. I have not yet seen the book, but A. N. Clements in his review in Nature (236: 357-8) writes as follows: "The author emphasizes that mosquito species are composed of partially isolated and largely non-interbreeding populations, which can differ greatly in their relationship with man."

Geographic Range and Diversity

My remarks about species and their ranges will be mainly speculative. Many North American biting flies have wide ranges, some of them from coast to coast and through many kinds of terrain. We know very little of the changes that may take place in biting fly populations over such ranges. *Simulium venustum* may bite in some places, and in others apparently not; *Culiseta inornata* from Lethbridge can be readily cultured in the laboratory, but not those from Guelph; and the swarming behaviour of *Aedes flavescens* differs between Manitoba and British Columbia. Very few cases of geographic variation have been studied systematically but there are interesting papers on *Culicoides variipennis* by Wirth and Jones (1957), on *Aedes atropalpus* by O'Meara and Craig (1970) and on *Culicoides* subgenus *Selfia* by Atchley (1970).

The extensive taxonomic study of *Culicoides variipennis* showed that it consists of five geographic subspecies, or better perhaps (Ross 1962) of four incipient species and a complex area of hybridization. All but one of these entities are western. The complexity of the fauna and flora of western North America, matching the complexity of the geography and the physical environment, is well known. Angiosperm genera such as *Gilia* or *Clarkia* have blossomed into considerable flocks of intimately related species at the hands of the Californian experimental systematists. Black flies in the west are evidently relatively species-rich in many subgenera, and we might expect an even greater diversity on the level of cryptic species and sub-species. It would be very interesting to make crosses of the eastern and various western forms of many of our common biting flies—*Culicoides crepuscularis* or *Culiseta inornata* for example. Goldschmidt (1934) carried through a project of this type on an extensive scale with the palaearctic moth, *Lymantria (=Porthetria) dispar*. All races, from western Europe to Japan, mated and gave offspring, and the males were always fertile; but the females of crosses between east Asian and European races became sterile intersexes (semi-males) due to the higher 'potency' of the male-determining factors of the Asian stocks. In crosses between certain Japanese races and the extreme western (Portuguese) form, the prospective females became not merely intersexual but fully sex-reversed phenotypic males functioning as such. Here we have a degree of sexual unbalance between the 'races' of a 'species' that would seem to provide the perfect material for the genetical control (eradication) of the sensitive populations (see Downes, 1959, 1965b). There are many examples among the Lepidoptera of intersexes, abnormal sex-ratios and similar phenomena in interracial crosses, and the cases mentioned in the preceding section indicate that the same is true also of the biting flies. It is likely that many more such cases would be discovered if systematic experimental crossings were made with geographically well separated stocks.

It is interesting to note that allopatric forms showing only slight visible differences are treated in normal taxonomic practice as geographic forms of the one species. It seems however that this remains a pure assumption except in the few cases in which experimental test has been made. The extent of the divergence that has occurred between the various populations in 'species' of wide, or transcontinental, or circumboreal, range remains, in general, unknown.

There is a special form of geographic diversity that is exhibited more clearly and fully in North America than perhaps anywhere else in the world. From the Gulf Coast (lat. 30°N) to the Arctic Ocean (lat. 70°N) and on through the Canadian Arctic Islands to northern Ellesmere (lat. 82° N) there is an almost continuous land mass without significant natural barriers, and many species have very considerable latitudinal ranges. Over this great extent, however, one important feature of the environment, length of day, varies continuously and with strict regularity from south to north. As is well known, a response to length of day determines both the seasonal life cycle of many biting flies and their daily pattern of activity. Differences in these responses must have a certain genetic basis. Here is a wide field for exploration, on which a start is being made (e.g. Depner and Harwood 1966). The environmental differences are large, and must impose great differences in the insects. At mid-summer, the length of the day at lat. 30° is about 14 hours; here, at lat. 53°, about 17 hours, and at the Arctic Circle, 24 hours; and north of the Arctic Circle the sun is continuously above the horizon for a period that reaches 4½ months at lat. 82°, thus extending over the whole season in which metabolic activity is possible. It is obvious that adjustments of the mechanisms involved must be very extensive, especially in the middle zone (say lat. 50° – 70°) where the rate of change of day-length at comparable stages in the growing season is so considerable. Yet *Aedes impiger* (*'nearcticus'*) ranges from about 38° – 82°N (Jenkins 1958) and *Eusimulium baffinense* from about 40° – 70° (Shewell 1958). Some indication of the scope of these changes can be found in the changes in the length of the daily swarming period for mosquitoes. Swarming behaviour is often related to the intermediate light intensity of the crepuscular period, and in the rapid twilight of the tropics typically lasts about 20 mins; at Ottawa (lat. 45°) 1 – 2 hours; at Churchill (lat. 58°) it is spread over about 6 hours and in the earlier part of the period waxes and wanes according to the extent of the cloud cover; and in the permanent daylight of the high arctic it can be observed in any part of the diel and depends mainly on favourable conditions of temperature and wind (Downes 1962 and unpublished).

The extent of the behavioural changes is evident; but whether these changes usually involve genetical adjustment of only a trivial sort, or on the subspecific or specific level, is not yet known.

Polytypic Species

The fourth, and last, problem area that I wish to draw attention to is this: the 'species' as identified, and even if it is in fact a true biological species, is not necessarily a homogeneous group but often shows great diversity, either throughout or as a characteristic of one particular section. A species, therefore, may be polymorphic or polytypic. And the disconcerting fact is that the diversification may affect important life processes and, in biting flies, often the very processes that we are most interested in from a practical point of view, such as biting habits, dispersal, or timing of the emergence.

One of the best known of these phenomena in biting flies is *autogeny*, the development of the oocytes from the unyolked condition to maturity on internal reserves, without the need for the blood meal that usually initiates ovarian maturation. It is a rather considerable change, involving the re-timing of the blood meal, the initiation of the maturation by a different stimulus or trigger, the retiming of the hormones necessary for egg maturation, storage during the larval stage of all materials needed for egg ripening, and the liberation of these materials from tissue storage rather than a dependence, in whole or in part, on the digestion and metabolism of the blood meal.

Autogeny is found in many different forms or grades (see Downes 1971). In *Aedes atropalpus* it characterizes one geographical sub-species, the most northerly of the four now recognized. In *Culex pipiens* it characterizes a series of local populations, predominantly populations closely associated with man, that exist widely scattered through the range of the sub-species *Culex pipiens pipiens* and sometimes closely contiguous with blood-meal-dependent but structurally identical populations. In *Culex tarsalis* it exists in a certain small proportion of individuals in nature, and in the laboratory a uniformly autogenous stock can be developed by selection (Bellamy and Kardos 1958). In *Aedes taeniorhynchus* the proportion of autogenous individuals fluctuates from place to place, and in the laboratory can be modified, within limits, through the nutrition of the larvae; the genetic factors that control egg maturation in this species evidently have an incomplete penetrance that can be modified somewhat by environmental conditions. Rubtzov believes that a similar situation is common among the black flies in the Russian taiga, the considerable differences in biting rate from year to year reflecting the differing nutritional conditions of the larvae. Finally autogeny may be a facultative condition of the adult individual; *Aedes impiger* in the high arctic passes through a first, blood-meal-dependent phase and later if it has been unsuccessful in finding a host passes into a low-fecundity autogenous phase by resorbing the contents of most of the ovarioles while egg development is initiated and goes to completion in a very few.

Thus autogeny is exhibited at many 'systematic' levels, from facultative in the individual, through various kinds of polymorphism to a sharply defined phenomenon in polytypic species. It occurs also at and beyond the species level. There are relatively few purely autogenous species of mosquitoes, but considerable numbers are known in *Culicoides*, in Simuliidae, and in Tabanidae, and in some cases the autogeny is reinforced by structural reduction in the mouthparts that renders the insect unable to take a blood meal. In Canada autogenous species of black flies and biting midges are frequent in boreal and especially in the true arctic life zones, and it is evident that they represent an adaptation to conditions that would make an extended flight in search of hosts chancy or difficult (Downes 1962, 1965a). This is not to say that autogeny is not a valuable insurance against the risks in obtaining a blood meal in other environments also; indeed it is evidently of significance both on the open prairie and in treeless coastal swamps.

Clearly autogeny is a phenomenon intimately related with systematics, in the areas of polymorphism, sibling species, adaptation and convergent evolution.

Spielman (1964) discovered both autogenous and blood-dependent populations of *Culex pipiens* living together in pools in a rather restricted urban environment, the utility tunnels beneath a group of large buildings. The two biotypes were readily interfertile in the laboratory, but in nature almost all females collected proved to be either homozygous for autogeny or homozygous for blood-dependence; less than 2 percent heterozygotes were observed. Thus a considerable degree of reproductive isolation existed. The isolating mechanism appeared to be a behavioural difference that led to assortive mating, individuals of the blood-dependent biotype (presumably of whichever sex) flying out from the larval pools to mate in a swarming flight some distance away, while those of the autogenous biotype mated without dispersal beside the larval habitat. Brust (1971) has recently shown that a similar difference in mating habits obtains between the autogenous and blood-dependent forms of *Aedes communis*. Lewis Davies (1961) demonstrated the same contrast of quiescence and dispersal in the black flies *Prosimulium fuscum*, an autogenous species, and the closely related sympatric but blood-dependent *Prosimulium mixtum*. In the autogenous species *Culicoides riethi* and *Simulium decorum*, it has been observed that the females may be egg-ripe at mating, whereas in most biting flies mating takes place when the ovary is in a quite undeveloped condition. Indeed, a restriction on dispersal and a strong tendency to inbreeding would be expected generally in autogenous forms, in which ovarian development begins soon after emergence from the pupa, because as a general rule female biting flies are quiescent while egg maturation is in progress.

I think therefore we can propose as a general hypothesis that autogeny is typically associated with inbreeding and tends to establish reproductive isolation vis-à-vis the normal, blood-dependent, form. It is a mechanism that inevitably tends to promote speciation, and it should be no surprise that so often the difficult environments, difficult that is in terms of the active flight and dispersal of typical biting flies, tend to be filled by autogenous races or species.

But interesting as this idea may be, especially when engaged in the study of a large fauna on a continental scale, it strays somewhat beyond the main point. Here I am using the phenomena associated with autogeny primarily as an illustration of the very large real differences that may occur within the customary unit – the species, or sometimes the sub-species – recognized by the taxonomist. We have seen that autogeny, the change from a blood-meal-dependent to a blood-meal-independent biotype, is accompanied, probably of necessity, by a change in (limitation of) the habits of flight and area of dispersal, and the circumstances of mating. In *Culex pipiens* moreover, a species that in its typical form hibernates before feeding in a state of reproductive diapause, it is accompanied further by an inability to enter this state of diapause and thus an inability to overwinter in the adult stage in cold climates, except in protected domestic conditions. Thus within a population that is not divisible by any known structural feature or in any other way used by the taxonomist, there may exist differences with regard to blood-feeding, ovarian development, dispersal, mating behaviour, association with man and the ability to hibernate – virtually the whole range of properties of a biting fly that have any practical significance.

To sum up: There appear to be many more species and semi-species of biting flies than classical taxonomy has led us to suppose. They are real natural entities; the populations are more or less strictly independent and differ from one another in their place in nature. Even within a biological species there may be polymorphism in very important respects. There is no one way to recognize and distinguish these various forms; anatomy, cytology, genetics, geography, ecology and physiology all make a contribution. The limited anatomical studies usually employed in systematics are not sufficient to discover the diversity that really exists. These problems can be met only by a radically updated approach to systematics with full use of laboratory and experimental methods.

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FLIGHT ACTIVITIES OF MOSQUITOES WITH EMPHASIS ON HOST SEEKING BEHAVIOUR

M. W. Service
Liverpool School of Tropical Medicine
Pembroke Place
Liverpool, England

A number of studies have been made on one or more of the series of events leading from adult mosquito emergence to blood-feeding and oviposition. Such studies, however, have largely been piecemeal, in that they have been on very limited periods of activity in the chain of events comprising the adult's life. The majority of such investigations have concentrated on the behaviour of mosquitoes at bait. There is little information on what mosquitoes actually do in between emergence, host seeking and oviposition. Our knowledge of adult mosquito behaviour is largely derived from taking samples of the population. This approach is of course common to studies on other biting flies, but Bursell (1970) recently concluded that any significant advance in the study of tsetse dispersal might have to wait the development of techniques that would enable the activities of individual flies to be followed in their natural environment. We are a long way from evolving such techniques and must for the present still rely on results obtained from a number of, usually discontinuous, samples. However, by improving sampling procedures, developing new techniques, and channelling ecological studies into less known spheres of adult activity, our knowledge on the behaviour of mosquitoes should profitably be advanced.

The purpose of the present paper is twofold. Firstly, to bring together information I have recently obtained on the movements and behaviour of mosquitoes in southern England, and secondly, to draw attention to the numerous, and often large, gaps in our knowledge of the behaviour of adult mosquitoes. Although this paper is centred on European mosquitoes I think a number of the problems and aspects of behaviour discussed will apply to Canadian species.

Behaviour After Emergence

Much of the information presented here concerns *Aedes (Ochlerotatus) cantans* (Meigen), a common Palearctic mosquito that readily bites man and a variety of mammals, and in certain areas is a vector of Tahyna virus (Aspök and Kunz, 1967). Typical larval habitats are shaded, shallow woodland pools and ditches. It overwinters firstly in the egg then in the larval state, adults begin to emerge in late April or early May.

The build up and decline in numbers of emerging adults has been measured by a variety of emergence traps. It was found that the emergence of adults was accompanied by the appearance of predatory flies such as Empids and Dolichopodids at larval habitats. They were seen to prey on emerging *Ae. cantans* during the daytime and also at dusk when maximum mosquito emergence took place. I have also observed predation by various Muscids, Dolichopodids, Ephydrids (Diptera) and Lycosid spiders on emerging adults of the *Anopheles gambiae* complex (Service, 1971*a*; 1972). Although predation at the beginning of adult life has sometimes been recorded in other species I think its importance, at least in many instances, has been overlooked. To evaluate the impact of this type of predation serological techniques were used. Antisera to both *Ae. cantans* and to species A of the *A. gambiae* complex were prepared in rabbits by a series of intramuscular injections of mosquito antigen (Service, 1973). Suspected predators were collected and their gut contents removed and expressed onto filter paper. These gut smears were then soaked in normal saline and interfacial precipitin tests performed on the extracts. A positive reaction in the form of a precipitin ring showed that a predator was involved. Results have shown that there is considerable predation on emerging adults of *Ae. cantans* by adult Diptera.

After emergence the adult population of *Ae. cantans* was sampled by human bait catches and by suction traps, which sampled 634 m^3 air per hour. A few unfed females and males of *Ae. cantans*, a high proportion of both having a clear solution (? sugar) in their crops, were caught in the suction traps a few days after emergence had started. Unfed females and males, also with a clear fluid in their crops, were also caught by sweeping the low-lying vegetation near the larval habitats. About 85% of the females were fertilized. In contrast, adults were not caught in human bait catches performed either near or some distance from larval habitats until about 3-4 weeks after the beginning of emergence. Almost all these females caught at bait were fertilized. This absence of a biting population of *Ae. cantans* following emergence has been repeatedly observed yearly for 5 years. A similar very marked interval between emergence and blood-feeding has been observed for 8 years in *Culiseta morsitans* (Theo.) and *C. litorea* (Shute) in a coastal area (Service, 1969*a*, and unpublished records). In this instance the build up of the emergent population was measured by collecting adults from outdoor resting sites. Initially only unfed females and males were caught, of which more than 60% had a clear fluid in their crops, but after 4-6 weeks blood-fed females began to appear. There was then a gradual but marked increase in the proportion of blood-fed individuals and a corresponding decrease in unfed females and males. Neither of these two species nor *Ae. cantans* is autogenous. It seems that after emergence only non blood-meals are taken, and it is tempting to speculate that at such times food is only required to provide the necessary energy for general flight activities, swarming and dispersal, and that only afterwards are the adults orientated to reproduction and therefore require blood-meals. Nectar feeding has been reported in *Ae. cantans* by Nielsen and Greve (1950), and Hocking (1953) has discussed the probable importance of nectar-meals in providing mosquitoes with energy. It nevertheless appears to be a long interval after emergence before gonotrophic activity starts. The extent to which this delay, between emergence and blood-feeding, occurs in other species is largely unknown, but I have some evidence that it occurs in *Anopheles claviger* (Meigen). In *Mansonia richiardii* (Ficalbi) the well defined interval between adult emergence and blood-feeding results from the species being initially autogenous.

Attraction to Bait

Bait catches have shown, not unexpectedly, that *Ae. cantans* and several other British mosquitoes, exhibit maximum biting activity at dusk (Service, 1969*a*; 1971*b*). Despite this, adults can be caught in large numbers at bait in sheltered areas at all hours of the day (Service, 1969*a*; 1971*c*). The reason is that unfed, and also blood-fed and gravid females and males, shelter during the daytime amongst grassy and scrubby vegetation. Although the unfed females resting amongst the vegetation are not actively host seeking during the day, they are nevertheless sufficiently stimulated when a suitable host arrives in their immediate area to feed on it. Daytime feeding can therefore be described as opportunistic. The first adults generally arrive within 1-2 minutes, there is then a rapid build up of females during the next 15-20 minutes, after which the numbers arriving fall to a low and more or less steady level (Service, 1969*a*; 1971*c*). This pattern of behaviour has also been observed in several *Culicoides* species, both in England (Service, 1969*b*) and elsewhere (Jamnback and Watthews, 1963; Gluchova, 1958), but is not universal as it does not occur in *Leptoconops bequaerti* Keffer (Kettle and Linley, 1967). In exposed areas where there are no suitable resting sites for mosquitoes or *Culicoides* no such biting occurs during the daytime, although environmental conditions may be favourable. After dusk, however, when both mosquitoes and *Culicoides* are actively host seeking, adults are caught biting in both sheltered and exposed areas (Service, 1971*c*).

The presence of an initial high number of mosquitoes at daytime bait catches in sheltered areas can sometimes be used to get an approximation of the range of attraction of a host to resting females. For example, after the catch at one catch site has dropped to a low level, showing that the immediate population has been caught, another catch is then performed at a known distance. If another high initial catch is obtained then it indicates that the catch at the first site did not attract adults from the second site. This distance of attraction for some British mosquitoes to human bait appears to be about 7-10 m. In west Africa Gillies and Wilkes (1972) found that several freshwater mosquitoes were attracted to bait animals from about 7.5 to 22.5-30 m.

Behaviour at Bait

Adults of *Ae. cantans* approach human bait directly, without first settling on nearby vegetation, but in *M. richiardii*, pre-biting resting may occur (Service, 1969*a*). It is not known why females should rest, sometimes for as long as 18 minutes, on vegetation very near a suitable host before settling on it. This type of behaviour has been observed by others (Colless, 1956; Ribbands, 1946; Senior-White, 1953; Smith, 1958; Wharton, 1962). The arrival of mosquitoes at bait is not usually regular, but shows an aggregated or patchy type of distribution. That is, catches are characterised by intervals of several seconds, or minutes, with few or no mosquitoes arriving, followed by the sudden arrival of several adults almost simultaneously.

After females have alighted on a host they usually have an exploratory period lasting about 8-31 seconds before they start to penetrate the host's skin (Service, 1971*d*). Considerably longer periods are then taken in penetrating the host and engorging, so that the total time a mosquito spends on a human host varies between 2 and 4 minutes (Service, 1971*d*). The long time necessary for feeding is a disadvantage, as it increases the likelihood of the mosquito being squashed or preyed upon by various predators. I have seen Empids preying on adults of *Ae. cantans*, and other *Aedes* species, that were feeding on cattle. It is well known that tsetse flies are sometimes preyed upon while hovering over or settling on their hosts (Glasgow, 1963).

I have also observed that when there are large numbers of *Ae. cantans*, and other *Aedes* species, attempting to feed at the same time on cattle they tend to disturb one another. This may result in a relatively high proportion of interrupted feeds. Adults may either refeed on the same individual or on adjacent cattle. Interrupted feeding is epidemiologically important because refeeding on different individuals of the same species, or sometimes even on different species, increases the spread of mosquito-borne diseases. Some adults although not fully engorged when disturbed do not refeed, and this may result in the production of a smaller number of eggs. Thus, a direct density dependent factor may be operative, i.e. large feeding populations resulting in an increase of interrupted feeds and decrease in fecundity. Apart from any disturbance during feeding, adults often have difficulty in taking a blood-meal from certain hosts, especially birds and small mammals (Corbet and Downe, 1966; Danielova, 1962). I have often seen mosquitoes experiencing difficulty in feeding on rabbits, and also on cats, dogs and wood mice (*Apodemus sylvaticus* L.). If this results in a high proportion of interrupted feeds it may increase the incidence of disease transmission but, on the other hand the reverse may be true. For example, mosquitoes find it easier to engorge on comatose rabbits suffering from myxomatosis than healthy active ones; this may consequently reduce the spread of myxoma virus to healthy rabbits (Service, 1971*c*). Maximum biting by most mosquitoes is in the evening around dusk when rabbits and other rodents have left their burrows but are very active, thus making it difficult for mosquitoes to get a blood-meal. This is in contrast to ornithophilic species feeding at this time, since in the evening most birds will be relatively inactive in their nests. Many of those species feeding on rabbits will feed on cattle if they are available, and it will be easier for mosquitoes to engorge on these animals in the evening since they will be relatively inactive.

Flight Activities After Feeding

After feeding mosquitoes sometimes seem to fly off with difficulty, and it has been reported that they usually rest on nearby vegetation after feeding (Shemanchuk, Downe and Burgess, 1963; Edman and Bidlingmayer, 1969). I have not observed this; on the contrary, blood-fed adults seem to fly off near the ground to disappear into the distance. Neither have I collected any blood-fed adults when vegetation has been sweep-netted near cattle in which adults have been feeding (Service, 1971*c*). Blood-fed adults of several species have in fact been collected 3-4 km from the nearest host (Edman and Bidlingmayer, 1969; Service, 1969*a*). The location of natural outdoor resting sites of mosquitoes, *Culicoides* and

Simulium species, has often proved remarkably difficult. For example, although Muirhead-Thomson (1956) encountered large biting populations of *Aedes* species in wooded areas in southern England, he failed to find any blood-engorged adults. Fortunately I have had better success. Based on collections and observations made during the past 8 years in various localities in southern England, there appear to be at least two distinct types of outdoor resting sites used by mosquitoes. Males and females in all gonotrophic stages of *C. morsitans*, *C. litorea*, *C. annulata* (Schrank), *A. plumbeus* Stephens and *A. claviger* have been found resting in cracks and hollows of trees, especially willow trees (*Salix fragilis* L.). The first four species have also been collected from under the outdoor eaves of derelict farm buildings and outhouses (Service, 1969*a*). These species are rarely caught when vegetation is sweep-netted. In contrast, adults of *Ae. cinereus* Meigen, *Ae. punctor* (Kirby), *Ae. detritus* (Haliday), *Ae. cantans*, *Ae. annulipes* (Meigen), *Ae. flavescens* (Müller), *Ae. dorsalis* (Meigen) and *M. richiardii* rest amongst scrubby or grassy vegetation. Some types of vegetation are unattractive, for instance few or no mosquitoes are collected from bracken (*Pteris aquilinum* (L.)) or young birch (*Betula pubescens* Ehrh.) saplings, whereas large numbers of adults rest amongst heather (*Erica cinerea* L., *E. tetralix* L.), grasses and amongst leaves of holly bushes (*Ilex aquifolium* L.). However, the distribution of *Ae. cantans*, and most probably other species, can be distinctly patchy in what appear to be more or less uniform areas of vegetation (Service, 1971*c*). I have often searched for resting adults in rabbit burrows, but it was not until 1970 that I found any mosquitoes in them (Service, 1971*e*). Since then I have found a number of *Aedes* species, including *Ae. cantans*, in rodent holes, but only during very dry weather. It appears that they normally rest amongst vegetation but under adversely dry conditions they retreat to more humid and protected resting sites, including rodent holes. In Poland Dabrowska-Prot (1961) found many more mosquitoes resting amongst vegetation in humid habitats than in those that were drier.

In England blood digestion in *Aedes* species takes about 5-8 days during the summer months. Although the minimum interval between successive blood-meals is therefore relatively long, there is very little information on what the mosquitoes do during this period of apparent inactivity, except that they move to more shaded areas if their resting sites become exposed to direct sunlight (Service, 1971*c*). Similar movements of daytime resting populations of *C. morsitans* and *C. litorea* have been observed (Service, 1969*a*).

In addition to predation on emerging adults, precipitin tests have clearly shown that spiders prey on mosquitoes resting amongst vegetation. In Poland a series of experiments have also shown that spiders can be important predators of mosquitoes resting in vegetation (Dabrowska-Prot, 1970; Dabrowska-Prot and Łuczak, 1968*a*, 1968*b*; Łuczak and Dabrowska-Prot, 1966). In temperate climates mosquitoes rest for comparatively long periods amongst vegetation, consequently predation during this phase in their life will probably be important in regulating population size. It is worthwhile to note that spiders and insects have been recorded as predators of tsetse flies resting on trees and amongst vegetation (Fiske, 1920; Chorley quoted by Buxton, 1955; Southon, 1959).

Repetition of the Gonotrophic Cycle

In tropical countries it is usually assumed that many species lay their eggs soon after becoming gravid, refeed at the earliest opportunity, and repeat this cycle with the minimum interval between successive ovipositions and re-feedings. In a few species at least this does in fact seem to happen, but in British mosquitoes there is no evidence of such a rapid repetition of events. In fact, nulliparous adults of *Ae. cantans* and *Ae. punctor* have been caught at bait 5-6 weeks after adults have stopped emerging. Nulliparous adults of *Ae. cantans* have also been caught at bait up to 6 weeks after they were marked at emergence. Examination of the tracheation of their stomachs showed that they had not previously taken a blood-meal. These results indicate that at least some adults have limited success in obtaining a blood-meal. Furthermore, large biting populations of *Aedes* and *Anopheles* species are often encountered in small woods, where precipitin tests have shown that rabbits are their main hosts. It is difficult to envisage that all these numerous adults can succeed in getting a blood-meal. Unfortunately the age grading method of Polovodova (1949) cannot be applied to *Ae. cantans*, as multiple dilations are not formed after oviposition and the number of adults having abortive oogenesis resulting in degenerating follicles is too low to be of much value. It is interesting to record that some

Canadian *Simulium* species apparently take up to two weeks to acquire a blood-meal (Davies and Peterson, 1956).

It is not known how quickly and efficiently gravid females find suitable oviposition sites, but I have seen adults of *Ae. cantans* ovipositing at dusk in the field on eight separate occasions. On arrival at the larval habitats adults spent about 1-3 minutes "testing" the soil and leaf litter before starting to lay. Oviposition took about 2½-4½ minutes, during which time *Ae. cantans* deposited about 30 eggs, mainly on the underside of leaf litter, within a very small area. There was no evidence of any preoviposition resting behaviour as reported in *Culex pipiens fatigans* Wiedemann by Mattingly (1966). Within about a minute of the end of oviposition, adults flew off into the distance.

I have not observed predation on ovipositing adults, but as predacious flies are usually present at larval habitats preying on emerging adults, it is likely that they also prey on gravid females.

Flight Activities and Levels

One of the advantages of suction traps is that they can provide information on flight activity of physiological categories other than host seeking females. The numbers caught can also be related to aerial density, e.g. number per 10^6 ft^3 (= 283 X 10^2 m^3) of air. However, because these traps are non attractive adult populations must be relatively large before a reasonable number are caught. Suction traps sample only the aerial population, consequently they will catch greatest numbers of the more active part of the population. In my catches unfed females of both mosquitoes and *Culicoides* have predominated (Service, 1971*b*, 1971*f*), giving further evidence that males, blood-fed and gravid females are relatively inactive.

When a number of suction traps were operated at different heights in a small wood it was found that the catches of *Culicoides* species and *Ae. cantans* decreased sharply with increasing height. Most were caught in traps situated 23 cm from the ground. In this particular wood *Ae. cantans* feeds predominantly on rabbits, and it seems reasonable that adults seeking either hosts or oviposition sites should be flying near ground level. In contrast, most adults of *C. morsitans* and *C. pipiens*, both ornithophilic species, were caught in the highest trap (550 cm). But from late August onwards, when females of *C. pipiens* stop blood-feeding and search for hibernation sites, both males and unfed females with fat reserves were caught in the lower traps (Service, 1971*a*).

When the catch was automatically segregated into hourly intervals the general flight activities of unfed *Culicoides* species and *Ae. cantans* were found to be very similar to their diel biting cycles (Service, 1971*b*, 1971*f*).

In the latest experiment eight suction traps have been sited in a wood in an approximate circle at a height of 95 cm. Three vertical strips of plastic mesh netting radiate out for 2 m from alternate traps. Although the size of the holes in the netting is sufficiently large to let *Chrysops* and smaller biting flies through, preliminary results have shown that traps with this netting catch more *Aedes*, *Chrysops* and *Culicoides* adults than traps without netting. Apparently adults orientate alongside the netting. Somewhat similar behaviour has been reported for *A. melas* (Theo.) by Giglioli (1964).

Limitations of Animal Baited Traps

Mention should be made of animal baited traps which have been extensively used for sampling mosquito populations and for virus isolation studies. Although undoubtedly useful they nevertheless may have severe limitations when unbiassed samples are required of the mosquitoes attracted to a particular host. In Nigeria, for example, a different composition of mosquito species was attracted to man depending whether or not he was enclosed in a bait-net (Service, 1963). Different types of traps may sample the population unequally. For example, many more individuals, and also species, were caught in a No. 10 Trinidad Trap (Brook-Worth and Jonkers, 1962) than in a cylindrical trap with inverted cone entrances when both were baited with dry ice (Service, 1969*c*). Furthermore, the presence of mosquitoes in an animal baited trap cannot always be taken as indicative that they are normally attracted to, and feed on, that host. Adults of *C. morsitans* and *C. pipiens* were caught in cylindrical traps containing a rabbit, very few fed on the rabbit, but when these traps were baited with chickens very few of these avian feeders were caught (Service 1969*c*). In many traps mosquitoes are prevented from feeding on the bait animal, consequently there is even less information regarding the suitability of the bait as a host.

CONCLUSION

The behaviour and flight activities of different mosquito species will most likely vary, and it is hazardous to generalise. Despite this I think it useful to summarise what appears to occur in some British anautogenous *Aedes* species, or at least in *Ae. cantans*. After emergence both sexes take non-blood-meals, mate and rest amongst vegetation, some adults may disperse to other areas. After this gonotrophically inactive period, which may last 2-3 weeks, females start taking blood-meals, but some females may experience difficulty in locating hosts and engorging. It is possible that a significant number may never obtain a blood-meal. After feeding, adults return to rest amongst vegetation where they are basically inactive, only moving if disturbed. Unfed females, including any that have been unsuccessful the night before in obtaining a blood-meal will feed on a suitable host during the day-time if it enters the immediate area. They will not begin active host seeking, however, until dusk. Very little is known as to when gravid individuals start searching for oviposition sites or whether they all succeed in egg laying, but oviposition itself appears to be quickly accomplished. During all these phases of activity adults fly very near the ground, but they possibly fly at higher levels for swarming and mating although I have not seen this, in fact I have twice observed swarming at a height of onlv 30-40 cm. There is little evidence of non-specific flight activity. I believe that *Ae. cantans* only flies for a particular purpose. There may be short flights to enable the adults to change their resting sites, to escape from predators, to feed on hosts in their immediate area etc., and longer flights for dispersal, host seeking and oviposition, in between these flights I think the adults are mainly inactive. This idea of a mainly inactive life is supported by the results of Graham (1969) who caught mosquitoes in a variety of traps in Canada, of which very few had the ovaries in stages III or IV of Christophers, thus indicating that there was little flight activity of these adults.

It is clear that we still know little about what mosquitoes do all day, and night, and I think it would be both rewarding and worthwhile to study this aspect of their behaviour further. Such studies might best be undertaken in small woods supporting large mosquito populations, but which are surrounded by exposed low lying vegetation, such as grassland or agricultural land. Under these conditions I think the mosquitoes in the wood can be regarded as a more or less closed population, and it should be easier to study the behaviour and activities of such an isolated population from which there is little, or no, emigration or migration.

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DISTRIBUTION OF *AEDES* MOSQUITO LARVAE AND THEIR CONTROL

R. A. Brust
Department of Entomology
University of Manitoba
Winnipeg, Manitoba

Temporary pool *Aedes* are the primary pest mosquitoes to be found in Canada. This presentation deals with those species of importance in southern Manitoba. The ecological principles presented, hopefully, are of general importance in understanding the distribution of mosquito larvae elsewhere.

Predation and parasitism are said to be important factors in limiting the numbers of mosquito larvae, but with regard to *Aedes* in Manitoba at least, there is little evidence to prove it. *Aedes* larvae are generally the only aquatic animals present in the pools between egg hatching and the emergence to adults, so predators cannot be considered a limiting factor. The work of Baldwin, James and Welch (1955) and James (1961), has shown that many insect predators do prey on mosquito larvae. However, the predators studied are dependent upon permanent water for development, where few *Aedes* larvae occur.

Parasites may be more effective than predators in controlling *Aedes* larvae, especially those that have an egg stage or a spore stage that can resist some drying in temporary pools and whose life cycle can be synchronized with that of the mosquito. Mermithid nematodes are the most likely candidates at present. The work of Chapman *et al.* (1967) and Peterson *et al.* (1967) emphasizes the potential use of nematodes for mosquito control. These workers have developed rearing techniques for several mermithids and have field tested these around Lake Charles, Louisiana (Chapman, H.C. personal comm.).

The study by Smith (1970), of the mermithid found in *Aedes impiger* at Baker Lake, N.W.T. is also encouraging. He found fairly high levels of natural parasitism in about 50% of the pools studied. The life cycle of the nematode appears to be well synchronized with that of the mosquito.

The effectiveness of microsporidia, in controlling *Aedes* has been studied by Kellen (1962), Kellen *et. al.* (1966) and Anderson (1968). They showed that in California, Louisiana, and Connecticut respectively, that usually 1% or less of *Aedes* larvae were parasitized. The highest level was 5%. This cannot be considered a limiting factor by itself.

At the present time, control of temporary pool *Aedes* in Manitoba is dependent upon the judicious use of short-lived insecticides, such as Abate for larvae and Flit MLO or Pyrethrum for pupae, applied from the ground to those pools that are heavily infested with mosquitoes. The area of treatment is small when only the producing pools are treated. Aerial treatment with insecticides, using fixed wing aircraft, can be hazardous to all forms of life since in most larviciding programs materials such as Fenthion, Dibrom, Malathion, Dursban, Gardona, or Abate are used over large acreages where some larval sites are known to occur. According to a detailed survey by Dixon and Brust (1972) only 3% of the uncultivated land area around Winnipeg was involved in mosquito production. Hence 97% of the land normally treated by aircraft would receive toxic insecticides where none are required.

In the Winnipeg area we found a very definite association between the abundance of *Aedes vexans* larvae, the most abundant and annoying human pest mosquito, and the proximity to a major adult blood source such as beef and dairy cattle. Larvae were often concentrated within a few hundred yards of feedlots where hundreds of cattle are housed in a limited space. Few concentrations were found to be more than ½ mile from the adult blood source. This source also included horses and swine in two locations around Winnipeg.

The concentration of larvae in a few areas is of particular importance when a larval control program is attempted. Following a general rain, time for surveying the pools is limited to 5-7 days before a new brood of mosquitoes emerges. A large survey crew is also very costly. Knowing where 90% of the larvae are going to appear, is a distinct advantage. The pools close to dairy and beef farms can be surveyed first, and those pools containing larvae can be treated by a ground crew. We found that the pools producing large populations of larvae were generally small in size, and were located in roadside ditches accessible to ground crews.

Two extensive larval surveys were conducted in Winnipeg environs. The first survey (1967) extended beyond the perimeter highway which surrounds metropolitan Winnipeg (See Fig. 1, Dixon and Brust, 1972). The survey area was 55 miles, by 2 miles, completely encircling the city. The area was divided into 5 sectors, and each sector was small enough so that one man could sample all the pools in one day, and complete the 5 sectors in one week. Eight complete surveys were carried out from May to August.

The second season (1968), the survey area consisted of 8 one-square-mile plots. Four plots were located outside and 4 inside the perimeter highway surrounding Winnipeg. Six complete surveys were carried out from May to August.

During the first sampling period, both seasons, all pools in the survey area were recorded on a large scale map (4 inches to the mile). Each pool was drawn to scale, and assigned a number. Subsequent samplings generally involved fewer pools, and hence the initial map served to identify the pools. At the first sampling, and each subsequent sampling, the pool dimensions, number of larvae per dipper of water, temperature and pH of the water were recorded at the site. When larvae were found, a sample was returned to the laboratory for identification. Generally 10 larvae were identified per pool. Sampling was repeated after each rainfall.

Estimates of larval abundance were obtained by taking aliquots with a pint dipper. The water in the pool was stirred gently prior to sampling. Three aliquots were taken from small pools, and 10 to 20 from large (> 50 sq. ft.) pools. The water volume of each pool was calculated from the dimensions taken at each sampling. The depth was measured at various locations in the pool, and an average depth was obtained.

Preliminary tests showed that the estimate of larval density was closer to the absolute density when water volume rather than surface area of the pool was used in the calculation. This is because once the surface of the water is disturbed, larvae disperse vertically. A capture, mark, release, recapture technique for estimating absolute density was not practical in our study. We sampled an average of 15-20 pools per day which allowed little time at each site.

A system of pool classification, based on permanence of the pool was devised so that those supporting large populations of larvae could be identified and studied in more detail: A. very temporary, water present for less than one week in summer; B. temporary, lasting 1-2 weeks; C. semi-permanent, lasting 3-5 weeks; and D. permanent. In practice, there had to be some flexibility in the classification, as one season had twice the average rainfall and the other only one-half the average rainfall. Pools that are permanent or semi-permanent one season may be temporary during another.

The maximum number of inundated pools occurred in the spring (Table I). Accumulated snowfall generally melts within a week at Winnipeg, and runoff water is not absorbed by the frozen ground. Pools so formed remain for a month or more, even in the absence of rain. Not all pools are suitable oviposition sites for adults. Throughout the season, only an average of 25% of the pools sampled produced one or more broods of larvae (Table I).

The species occurring in the largest numbers were *A. vexans, A. fitchii* and *A. flavescens* (Tables II and III). *Aedes spencerii, A. dorsalis* and *A. sticticus* were localized and these species were troublesome as adults

TABLE 1

Phenology of mosquito development in the survey area during 1967, and a record of the number of pools infested with larvae

Dates	No. of pools per sector of the survey area[a]					Total no of pools	No. of pools with mosquito larvae and pool type[b]	% pools infested
	A	B	C	D	E			
May 23-30	33(8)	29(14)	22(12)	15(3)	20(8)	119	45 (36B, 8C, 1D)	38
June 1-7	19(0)	26(10)	16(10)	13(0)	16(3)	90	23 (17B, 5C, 1D)	25
June 8-15	12(0)	21(0)	14(0)	8(0)	8(0)	63	0	0
June 18-25	11(0)	20(0)	12(0)	7(0)	6(0)	56	0	0
July 10-17	10(1)	14(6)	17(11)	12(6)	6(1)	59	25 (9B, 4C, 12D)	42
July 18-28	8(0)	11(3)	12(7)	11(5)	5(0)	47	15 (4B, 1C, 10D)	32
August 6-18	6(0)	8(0)	11(6)	11(6)	6(2)	42	14 (8B, 6D)	33
August 21-28	2(0)	6(1)	6(4)	7(3)	3(0)	24	8 (1B, 3C, 4D)	33

a) Parentheses show pools infested with larvae.

b) See text for pool description.

TABLE 2

Larvae of mosquitoes in the 1967 survey area

Species	Sampling dates and the abundance of each species given as a percentage of the total		
	May 23-June 7	July 10-28	August 6-28
Aedes fitchii	70.2		
Aedes flavescens	15.7		
Aedes campestris	7.8	0.18	
Aedes riparius	2.3		
Aedes canadensis	0.4		
Aedes excrucians	0.3		
Aedes sticticus	0.1		
Aedes communis	0.1		
Aedes barri	0.002		
Aedes spencerii	0.2	4.08	
Aedes dorsalis	1.8	3.7	
Aedes vexans	1.04	88.03	3.3
Aedes nigromaculis		0.28	
Culex tarsalis		3.9	84.4
Culex restuans			7.4
Culiseta inornata			4.9
Estimate of the total number of larvae in the survey area	4 million	10 million	400,000

in some areas. *Culex tarsalis, Culex restuans* and *Culiseta inornata* made up a large proportion of the larvae during late July and August, as occurs in Alberta as well (Happold 1965) but the larval population was small compared to earlier in the summer. *Culex* and *Culiseta* adults are not troublesome as human pests during August, and hence are not part of the control program strategy in Manitoba.

In the 1968 survey area, where 8 one square mile plots were surveyed 6 times, only 20% of the pools produced one or more broods of larvae (Table IV). More research into what makes certain pools attractive to adult females is urgently needed. Both years, 1967 and 1968, the areas of high larval density were located near cattle, swine and horses.

The amount of rainfall is important for hatching eggs and creating pools that will remain for 2-3 weeks. During both seasons, the peak of each larval population was reached 7-10 days following precipitation levels of 2 inches or more. One inch of rain or less did not produce larvae. Hatching of eggs laid at the bottom of pools can occur following one inch of rain, but pools so formed generally dry out before larvae complete their development.

The reasons why some pools are selected, and others are not include the following: (1) some are more chemically attractive to ovipositing females

TABLE 3

Larvae of mosquitoes in the 1968 survey area

	Sampling dates and the abundance of each species as a percentage of the total				
Species	May 27-June 7	June 10-13	July 8-10	August 6-8	August 20-28
Aedes vexans	92.45	3.5	86.6	58.3	91.83
Aedes flavescens	1.50				
Aedes fitchii	2.93	91.1			
Aedes nigromaculis	0.65		2.8		.40
Aedes dorsalis	2.01	4.5	5.9	33.2	.13
Aedes spencerii	0.41		0.2		
Aedes campestris			4.5		.01
Culiseta inornata	0.03	0.8		7.4	7.60
Culex tarsalis				1.1	.02
Estimate of the total number of larvae in the survey area	9,000,000	16,000	3,000,000	12,000,000	172,000,000

TABLE 4

Phenology of mosquito development in the 1968 survey area, and the number of pools infested with larvae

	Square mile plots[1]									
Dates	Wo	Wi	No	Ni	Eo	Ei	So	Si	Total no. of pools	% pools infested
May 27-June 7	17(10)	19(4)	28(12)	26(4)	27(4)	20(1)	31(4)	10(0)	178(39)	22
June 10-13	6(0)	13(0)	20(3)	22(1)	23(0)	20(0)	18(0)	5(0)	127(4)	3
July 8-10	7(3)	16(0)	21(9)	20(5)	26(15)	22(5)	24(2)	12(0)	148(39)	26
July 18-19	6(0)	14(0)	20(0)	22(0)	23(0)	21(0)	23(0)	12(0)	141(0)	0
August 6-8	5(1)	9(0)	23(2)	25(2)	24(2)	18(2)	31(9)	13(0)	148(18)	12
August 20-28	22(6)	26(0)	30(8)	36(4)	23(17)	24(3)	44(16)	–	205(54)	26

[1] Parentheses show no. of pools infested.

(Hudson and McLintock, 1967, Maw 1970, Osgood 1971); (2) some are close to plant cover which provides suitable resting ground for gravid females (Bodman and Gannon, 1950) and (3) some are close to an adult blood source (Horsfall 1942, Dixon and Brust, 1972).

The repetitive use of pools by the same or different species is a very important factor in identifying larval developmental sites, and oviposition sites. In our study, 20-25% of the pools sampled produced larvae. Of these 56% produced one brood, 32% two broods, and 12% three broods. The pools that produced univoltine *Aedes* during April and May, were also the important pools for the production of *Aedes vexans* during June, July and August. Eggs of *A. vexans* are present in the pools during April and May, but they do not hatch in snow-melt water (Brust and Costello, 1969). Mapping of producing pools can be started early in the season, so that in a control operation survey crews can update their maps long before populations of *A. vexans* appear. Univoltine species are not generally abundant enough to warrant control around Winnipeg. This situation is different in the forested regions of the province.

The area of the pools which produce mosquitoes, in relation to the region as a whole, is also an important factor in control. We found that the production of mosquitoes occurred in only a small portion of the total area. In 1968, the total area of producing pools amounted to 5 acres out of the 5120 acres surveyed. Since the survey was primarily on agricultural land, only ditches, farmyards, bush areas and pastures, or approximately 150 acres made up the potential habitat. The area requiring larval control measures was 3% of the uncultivated land area. The 1968 season was the wettest in the last decade, therefore even less area would be involved in mosquito production during an average season.

Edman and Downe (1964) showed that cattle were the most important source of blood within a 5 mile radius of Manhattan, Kansas. Out of 1417 females of *A. vexans*, 902 had obtained all or part of their blood meal from cattle. Rempel *et al* (1946) have shown that cattle and horses are important hosts for *A. vexans* in Saskatchewan. Man was also a host in Urban areas. Shemanchuk *et al.* (1963) showed that cattle were the primary hosts for *A. vexans* and other mosquitoes in southern Alberta.

Nayar and Sauerman (1968) have shown that dense larval populations lead to developmental synchronization, and they suggest that these populations give rise to migratory adults. If true for *A. vexans*, dense populations at the source should receive priority where control programs are concerned.

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DISCUSSION

Discussion Leader . . . . G. DeFoliart
Discussants . . . . K. M. Sommerman
G. A. H. McClelland

DeFoliart: I would like to begin the discussion this afternoon with a couple of general comments. Yesterday the rapporteur, Dr. Corbet, said that what is needed most now are a few successes, or even one, and I certainly agree with this. It is disconcerting to realize that after 70-90 years of medical entomology, we have only one practical, non-insecticidal control method available, which, as Ernest Bay was telling us, is *Gambusia* in California rice fields. In this regard I think it is appropriate that Dr. Brust's paper came late in the meeting. If elimination of or reduction in amount of insecticide used, is part of this equation of biting fly control and environmental quality, as it surely must be, then I think, any operation which reduces the area of treatment by 97% qualifies as a very significant contribution to environmental quality. This type of approach is basic to and enhances the potential usefulness of all the non-insecticide methods about which we have been speaking. If we need publicity of our successes, then the project about which Dr. Brust spoke certainly qualifies as a deserving one.

The subject of communication or lack of it between entomologists and the public, on one hand, and high level research directors and those who control the purse strings, on the other, has arisen before. I think this is a problem of great importance, because both in academia and government we are losing, not just holding, but losing support. Somehow we have to find a way to convince administrators of the myriad of unsolved problems in entomology.

The paper by Mr. Downes pointed out that we may have more problems than heretofore realized. He estimated that we now know about one-fifth of the insects with which we are dealing. How do we get across this point of the great numbers and diversity of insects? Somehow we have to let the people who distribute the money know that each type of insect is a biological entity in itself. In my university we have a whole department devoted to one animal – the dairy cow – and I have a difficult time convincing the administrators that I have 200 times as many problems with 200 pest insects.

There has been some discussion about what we call these insects with which we work. Bob Peterson has discussed reasons why we should call them "man-biting flies" rather than just biting flies. In the interests of getting the public's attention we might even go one step further and refer to them as "man-eating flies" which, I think, might elicit more notice of our problems.

Sommerman: We are here to examine ways in which the control of biting flies can be reconciled with the preservation of environmental quality. Dr. Weidhaas has pointed out the progress made and the difficulties encountered in repellent research, but it still sounds hopeful so that is encouraging, especially for Alaskans. Most of the refinements pertaining to techniques, as mentioned by Dr. Service and Dr. Brust, are not applicable to the situation in Alaska today. But they will enter the picture eventually when the situation changes with the influx of more people, unless, great advances are made in other approaches to biting fly control.

The situation in Alaska is very simple, as it is in some areas of Canada where the interactions of biting flies, people and the environment are comparable. Cost is usually a decisive factor in determining the kind and quality of abatement action taken. Research and abatement activities are expensive per capita in Alaska because the human population averages one individual per two square miles.

Five groups of biting flies are involved and they are listed in descending order of health significance: mosquitoes, black flies, *Culicoides*, Tabanids, and snipe flies, which belong to the genus *Symphoromyia*, family Rhagionidae. These biting flies may be detrimental to health in at least four ways, – listed in ascending order of health importance: general nuisances; biting, blood-sucking pests; allergy inducers; and perhaps vectors of disease agents. None is yet a proven vector and therefore priority for "control" activity is low. Secondary infections may result from scratching, - especially in Native villages.

In each of the above kinds of biting fly injury, the activity is centered around humans and involves actual contact or close proximity. If chemists could develop an otherwise acceptable repellent that would prevent these flies from approaching closer than two or three feet, both the people and the environment would remain healthy because the repellent is applied to people or their clothing, and is not broadcast at large in the environment. Such a repellent would operate regardless of locality, hopefully, and its use would require no other knowledge of the insects or the environment. Development and use of such a repellent should probably receive highest priority in research.

In Alaska the common brands of topical repellents containing Diethyl toluamide (DEET), and Dimethyl phthalate (DMP) are effective in varying degrees against these biting flies, especially concentrations containing 50% of the active ingredient; though their efficiency seems to vary with the individual and with the group of biting flies involved. Protective clothing, whether repellent-treated or not is used by some and fortunately the temperature is almost always cool enough so extra clothing is comfortable. The DEET-treated net parkas and trousers, available commercially in Minnesota, are rather expensive and not well publicized, but it is claimed they remain effective about three months and enough DEET is supplied for one additional treatment. This should be sufficient for an entire season in Alaska. Use of repellent-treated clothing of this kind might become popular if it were publicized, and if, in each community, either a Pest Control Operator, or Dry Cleaner, or a small business were equipped to treat such outer clothing with repellents.

All other kinds of abatement activities require a knowledge of the target insect's habits in the immature or adult stage, and a knowledge of the associated environmental conditions. In addition application of chemicals requires a knowledge of the behavior of the pesticide in associated environmental conditions, and the effects of the pesticide on target and non-target organisms. The habits of the target insects (especially vector capabilities), the environmental conditions, including the presence of human pathogens, and the density of both the human and insect populations, all directly influence the health significance of the biting fly groups, as well as the choice and success of any "control" activity.

In Alaska, with reference to the insect's habits, except for a few species of warm-water *Simulium*, all the biting flies apparently have but one generation a year. The mosquitoes are most active the first half hour or so after sunset, and their daytime behavior in woods is also the same as that described by Dr. Service. In my experience the mobile funnel trap sampling after sunset produced almost all the blooded and gravid specimens I've taken, indicating purposeful flight at that time, as Dr. Service observed. In the forested regions the trees impede mass movement of the biting flies. Draining and filling habitats of the larvae are feasible only when done for construction of housing developments, but clearing woodland, brush and high grass from around dwellings reduces the mosquito threat by destroying the resting sites.

Environmental conditions have produced three bioclimatic regions in Alaska, which differ both in the kind and magnitude of the biting fly problem, and in the feasibility and kind of biting fly control. The Aleutian Islands are excluded from these three regions because the biting fly problem is minimal or absent there due to the fairly constant strong winds and lack of trees for shelter.

One of these regions coincides roughly with the coastal forest and extends eastward from Kodiak Island to the Canada Border near Prince Rupert. This narrow strip is limited by a marine environment on one side and snow-capped mountains on the other. The biting fly habitats are discontinuous and sporadic. Biting is sometimes a problem in localized areas for short periods depending upon the species or group involved. Since almost half the population of Alaska is concentrated here, especially in the Anchorage area, there it is considered feasible to adulticide for mosquito and *Culicoides* abatement. But it is no longer done because a few individuals always object and pilots are not willing to risk suit. Therefore no broadcast chemical control action is taken against biting flies in this region

The second bioclimatic region includes the moderate to sparse boreal forest of interior Alaska, which contains an extensive network of streams. The larval mosquito, black fly and *Culicoides* habitats, associated with these streams and adjacent wet lands, are rather extensive and fairly continuous. The larval tabanid habitats are sparse and limited to lowland basins where the adults are only occasionally troublesome. The larval snipe fly habitats occur in the southern half of the region and are sporadic because they are largely concentrated on timberline slopes with a SE, S, and SW exposure.

The human population throughout this region is sparse except on the large Military Base and in Fairbanks. There, as elsewhere in the Region adulticiding for mosquito and *Culicoides* abatement gives extremely temporary relief because of rapid reinfestation, so topical repellents are used to some extent anyway. In Fairbanks when mosquito abatement is deemed necessary, upon recommendation of the City Council the Public Works Department applies malathion with a thermal fogger. Malathion is the only chemical cleared for use in mosquito abatement in Alaska, but its effects on non-target organisms have not been tested. Its derivatives have been shown to persist in Interior Alaska soils for more than a month, and in some cases over a year. The Fairbanks mosquito abatement operation is controlled and executed by people who know little or nothing about the inter-relations of: – the environmental conditions, the behavior of the pesticide, and the habits of the target insects. Although mosquitoes are known to be most active during the first half hour or so after sunset, which may be 10:00 PM or later, adulticiding activities are scheduled at the operator's convenience, and often regardless of wind conditions, temperature, or even real need for abatement. After sunset, rarely is the temperature above 70°F, the minimal temperature for consistent kill. During one extremely dry summer when mosquitoes were no problem, routine mosquito fogging was even done for aphid control! These problems concerning abatement activities were also common in the coastal forest years ago when adulticiding was still practiced there in Anchorage.

The third bioclimatic region includes the tundra, a treeless area extending from Kodiak Island north, and east along the Arctic Coast to the Canada Border. On the Arctic Slope permafrost prevents drainage from snowmelt, and continuous daylight from May to August provides the light and heat necessary to convert this whole continuous expanse into a mosquito breeding area. Mosquitoes are the major pest and their populations are tremendous. The absence of trees enables a light breeze to carry them great distances. The other biting fly groups are rare or absent so have little or no health significance. Throughout the tundra the human population is sparse and composed mainly of Natives, except for the few whites associated with the oil operations.

Aerosol treatments in dwellings, personal repellents, and repellent-treated clothing are the only means of protection that are economically feasible in this region.

Although biting fly larviciding is generally considered more efficient than adulticiding, it is not done in Alaska largely because of the prohibitive cost, inaccessibility of habitats, and lack of trained people to do the work. Therefore most of the pertinent points mentioned by Dr. Brust are not yet applicable to Alaskan abatement activities. However, if all people did use repellents the blood meal source would be considerably reduced, which in turn would reduce egg production, hence mosquito production, near habitations, as Dr. Brust mentioned.

Since larviciding operations occur in the environment of the insects there is more chance of detrimental effects on parasites and predators, as pointed out by Dr. Service, and perhaps on non-target organisms also, than there is with adulticiding activities in the urban and suburban habitats of humans.

Dr. Downes has stressed a very important point about the shortcomings of present day taxonomy. Insects as well as people are the product of their heredity and environment so their names should also conjure connotations of the entire insect, its habits and habitats, and not just a few obvious, or not so obvious morphological characters. In other words, taxonomy and bionomics are inseparable. With present emphasis on environmental protection surely more field observations will have to be made, and the situation will eventually correct itself.

Since these biting flies all take nectar before their blood meals, perhaps a substitute nectar bait could be developed for use in traps placed near emergence sites to catch both sexes of adults. Such traps would have no direct effect on the aquatic habitats, but if successful they may produce a decline in wild flowers, if these flies are that important as pollinators, but then any such decline in wild flowers would tend to make the bait even more popular.

Again with reference to nectar feeding, it would almost seem as if it might be possible to capitalize on this one general habit and combine it with plant hormone research to modify the nectar chemically so the biting flies would not desire a blood meal, or so that egg development would be retarded

In Alaska and other places where similar conditions exist, the following action might be taken to reduce biting fly injury to humans and at the same time produce a minimal detrimental impact on the rest of the environment.

1. Promote the use of repellents and repellent-treated clothing.
2. Encourage research for the development of better topical repellents.
3. Encourage research for the development of a substitute nectar bait for use in trapping adults near emergence sites.
4. Encourage more field observations. They are the source of basic information, hunches and theories, which later are tested in laboratory investigations, not vice versa.
5. Promote legislation requiring people, who are applying broadcast pesticides for biting fly abatement, to know the habits of the species involved, the behavior of the pesticide in associated environmental conditions, including optimum conditions for its dispersal; and the proper operation of the equipment being used.

McClelland: First of all, I want to make some remarks about the individual presentations this morning and then go on to a few more general topics.

First of all, with Dr. Weidhaas's paper my general reaction was that the value of personal protection needs great emphasis, especially in the northern parts of this continent where the human population is sparse and the insects extremely abundant. This would seem to be certainly the most economical method that we have available at present or in the near future He mentioned the disparity between laboratory and field trials using combinations of lactic acid and CO_2 and one possible explanation of this seems to be something alluded to by Dr. Friend and Mr. Smith that a hierarchal sequence of responses may be involved. Olfactometers may thus be measuring a proximal response whereas the efficiency of a trap in the field depends more on long-range stimuli. This correlates nicely with Dr. Service's observations of bird feeders coming to a mammal trap.

Nothing was said about repellents for bloodsucking insects such as tabanids where the host-seeking response is primarily visual but I remember from personal experience (and Dr. Weidhaas may have some data on this) that application of a repellent which was quite satisfactory against mosquitoes seemed to have no effect on tabanids. Perhaps some repellents do work against tabanids. I would like to know more about this, how can one best repel the visual bloodsuckers? Another thought that has occurred to me regarding the use of repellents is that repelled mosquitoes or bloodsucking insects keep on seeking a host; in fact, they may become more avid as time goes on and I am wondering whether we have allowed our thinking to be too channelled along the line of repellents when perhaps we should be giving equal thought to attractants. Why not attract the bloodsucking insect in a way that would divert it from the areas where its bites are painful, disease-causing or a nuisance, and also kill it. I am thinking of a "super Hocking-blue-cap" or some strange device that would attract mosquitoes away from the face or hands to another part of the clothing where contact poison could be combined with the attractant agent – it is just a thought but there may be some profitable lines of research in this area.

Coming now to Dr. Downes, who raised many interesting issues. One point, however, may need clarification. He mentioned that we could not colonize many species of blackflies nor cross them nor run genetic experiments in the laboratory because they are difficult to mate under laboratory conditions. Perhaps he would explain to the non-geneticists how the presence of these inversions can imply reproductive incompatibility. In Dobzhansky's classic studies on *Drosophila pseudobscura*, seasonal variations in the frequency of inversions in the polytene chromosomes were not necessarily correlated with reproductive incompatibility. On that line, it may be of interest that one of Dobzhansky's former students, Francisco Ayala, now on the Davis faculty with him, has applied the method of starch-gel electrophoresis to the study of allozyme variation in *Drosophila*. Although this technique may tell a somewhat different story from a study of inversion polymorphisms it is much easier and quicker to extract the flies for electrophoresis than to prepare and read the polytene chromosomes. It is a technique that might well be applied to blackflies.

The cytoplasmic crossing types in *Culex* I do not believe can be regarded as species. Gene flow is possible, even if only one way: when crossing type A meets crossing type B it may take over and displace crossing type B but the genes that were present in the populations of both crossing types are incorporated in the new population. Laven suggested that there was however one theoretical possibility of speciation where three or more of these mating types arose together so that two different one-way crossing types each displaced a third crossing type until when they met there was complete reproductive incompatibility.

Dr. Downes's correlation between autogeny and inbreeding was an interesting statement and I was trying to think of the implications that autogenous insects were necessarily more inbred. All animals surely have to evolve some form of mechanism to ensure outcrossing. This is essential to the survival of any species so one wants to know what happens to the other insects that are not bloodsuckers; they are in a sense autogenous but they have presumably avoided the dangers of inbreeding, so I wonder whether autogenous mosquitoes are in fact so very different. Consider also the example of *Culex fatigans* in an African hut. This is not an autogenous form but in dry parts of Africa it is confined to the environment of a small hut where it breeds in jars of water and this seems to compare very closely with *Culex pipiens molestus*, the autogenous form, which is usually found in restricted habitats. The size of the habitat and the size of the population in both cases may be similar. Admittedly, in the case of *C. fatigans* the population can expand out when the rainy season comes but I suggest that at certain times of the year the autogenous *pipiens* populations can also expand in a similar way. However, Dr. Downes's point is very well taken that the taxonomists should be more concerned with biological species and I think to this end very many non-morphological characters should receive more emphasis. Here I think numerical taxonomy may well provide the method for integrating all these different and often quantitative characters.

An implication of the multiplicity of species for autocidal control is rather interesting. If there are in fact very many more species than we have hitherto thought, or if populations of some biting fly or mosquito perhaps turn out in reality to be a number of discrete genetic entities, the size of any one population and hence the magnitude of the autocidal control effort will be smaller. On the other hand, the more of these different genetic entities or biological species that exist together, the more difficult it will be to eradicate the whole lot because a completely separate genetic technology is going to be needed for each one. If we succeed in creating a suitable translocation or inversion in one, we would still need it in the others; the more species the harder the technology. It could be an advantage, however, in cases where only one of a species complex was a pest.

Coming now to Dr. Service's very interesting paper, my first comment concerns spider predation on emerging adults. I wonder whether it may explain some examples of strongly periodic emergence in mosquitoes. An example is *Aedes vittatus* in Africa which emerges at the hottest time of the day when the water temperature is sometimes as high as 42 degrees in the field. One might think that such predators as lycosid spiders on exposed water surfaces would take shelter at the hottest time of day. I have no personal observations on spiders but it might be interesting to see whether some of these circadian periodicities in emergence can be correlated with mechanisms for avoiding predation.

Mention of the long interval between emergence and first feeding is very interesting. Is this characteristic of most species in cold temperate climates or peculiar to only a few? Is there evidence that feeding begins earlier in any other species in cold temperate areas or is there comparable data on any tropical species? In view of this long lapse between emergence and bloodfeeding I wonder if Dr. Service can rule out the possibility of facultative autogeny in *Aedes cantans*. A comparable observation in California, which Dr. Anderson will confirm, was made by Duane Lee of Berkeley in a mark-release-recapture experiment (which I do not think is published yet) where *Aedes sierrensis* captured at about 56 days after initial release was still nulliparous or uniparous. This suggests that the phenomenon might be more typical at least among related *Aedes* species.

Is opportunistic feeding in sheltered areas really opportunistic or is it indicative of a light-intensity effect on biting periodicity? An analogous situation is found in the tropical forest where the periodicity of biting in the canopy is usually different from that on the forest floor. In the canopy biting periodicity can be extremely sharp, occurring in a period of perhaps half an hour or so at dawn or dusk, whereas on the forest floor a low level of biting may continue all day. Many of you will be familiar with the work of Haddow and others on this, so one wonders if in the sheltered areas there is merely a stretched-out biting period. While I cannot disagree with the concept of opportunistic feeding I think it is not the only explanation for these longer biting periods.

There have been recent observations that male mosquitoes have the same host-seeking behaviour as females. We have noticed it in *A. aegypti* using one of Harry Gouck's olfactometers similar to that used by Dr. Weidhaas and we have seen in the field, at Dar es Salaam, Tanzania, that males would come to the host and show the same response as females. In the olfactometer the males do not enter the traps, they stay in a little hovering swarm outside the entrance. If you run the olfactometer with males and count the number that get in the traps you do not get a true measure. If, however, you observe what is going on, you see that the males are nevertheless congregating outside the trap entrance leading to the host that is favoured by the females. Now the point of these remarks is that Dr. Service has mentioned certain dipteran predators that come after the biting insects and one wonders if perhaps the predators are also showing the same response. Just as male mosquitoes respond to the host to provide an opportunity for copulation maybe the predators respond to a host as a possible source of bloodsucking insect prey. It might be an interesting problem to investigate.

The question "Where do females go between feeding and oviposition?" is intriguing. We have often assumed rather readily that female mosquitoes take a single blood meal, undergo a gonotrophic cycle, rest during this gonotrophic cycle, and then oviposit. However, work that Gordon Conway and I did in the Buguruni auto-tire dump, one of these now famous stacks of tires showed conclusively that some females of *A. aegypti* engorged twice on consecutive days in the same gonotrophic cycle. The mosquitoes we released were fully and freshly engorged and, by engorged, we mean that their abdomens were thoroughly bloated and bulging with our own bright red blood. The next day a mosquito that was marked in this condition on the previous day was recaptured again fully engorged. Now one knows that 24 hours after a mosquito has fed it does not have the same bloated appearance. We had seven of these double feedings and one of them occurred in what was almost certainly not the first gonotrophic cycle because this particular mosquito had been caught, marked and released engorged on day 0, captured again and engorged on day 4, and captured again on day 5 when it engorged once more. One assumes that it had oviposited between its engorgement on day 0 and its capture on day 4 although we could not confirm this by dissection or we would have been unable to release the mosquito. So another possibility that must be taken into account with biting insects is that there may be more than one feeding in a gonotrophic cycle.

Coming to Dr. Brust's paper, I think Dr. DeFoliart has made several comments here and I will restrict myself to a few. I notice he mentioned the lack of larval predation and I am wondering, in view of what we have heard from Dr. Service, and as Dr. Anderson mentioned yesterday—Garcia's work in California on the predation of salt marsh *Aedes* by spiders as they emerged—whether surface predators might play any part in these pools. I think the thing that impressed me most about Dr. Brust's paper was the preponderance of larval breeding close to adult blood sources. This seems to imply first that (in this species at least) population size may be limited by the availability of blood and, second, that in areas where man is the main blood source, personal protection by repellents could in itself reduce the population. I wonder whether there are observations to confirm that.

Coming now to some general comments on the last couple of days, it seems to me that almost nothing has been said about population dynamics. I think we are all aware of the implications that most animals have a density-dependent mortality component. As examples among adult mosquitoes, Brust has shown that opportunities for feeding may influence survival and fecundity and Service has shown that interference can occur between mosquitoes biting the host at the same time. This might be related to the very sharp circadian periodicities of biting in some species. Could it be a mechanism whereby the maximum numbers of bloodsucking insects come to hosts simultaneously so that their interaction may possibly exercise a density-dependent control à la Wynne Edwards? Dr. Hocking has made many observations on aggregation among larvae and he might have something to say on its effect as a density-dependent mortality factor. We must not forget that, on average over the years, one female gives rise to one female irrespective of the number of eggs or batches of eggs laid, so when we are talking about achieving such and such a percentage kill this will not cause a linear reduction in the population if density-dependent mortality factors are operating.

You all know that chemical, biological, and genetic or autocidal control operate differently in relation to density. In chemical control, ignoring susceptible individuals which escape a lethal dose, there may be some resistant individuals that survive but resistant phenotypes often have lower reproductive potential or are less fit generally than the susceptible forms. In the case of autocidal techniques the chance survivors will in contrast tend to be thoroughly normal individuals which, having been exposed to a lower density, may respond with greater fecundity and the population may well show more homeostasis than under chemical control. I am sure that these factors are also important for biological control agents and should be given more emphasis. We might even seek ways of applying control agents to populations in such a way as to antagonize the natural population homeostasis.

One final comment I want to make on autocidal control which I do not think has been given enough emphasis in these few days. We have heard that most methods of autocidal control are going to involve inundative releases. I wonder whether enough has been said about the implications. Given the genetic technology, e.g., the availability of translocations, and given the mass production facilities needed, we have to face the fact that we are dealing with a vector that may have a dispersal of 10 or 20 miles or more. Certainly, if we ever develop techniques for blackflies we may have to be involved with very long distance dispersal. Releases have to be made on a front that is far deeper than the maximum possible dispersion and as broad essentially as the area of country in which the insect occurs. In Canada, which has a very sparse human population and a dense fly population in an enormous area, inundative releases would seem to be absolutely the worst possible choice of control method from an economic point of view. I grant you that this is a perfect method for preserving the environment but I doubt if such operations are ever going to be feasible in view of the potential productivity or wealth of the land which we are going to preserve from mosquito nuisance. I have sometimes been considered a mosquito geneticist and I hate to do this anti-public relations job for autocidal control. I think that the technique has many applications in other parts of the world where pest populations are smaller, more closed, or where the economic gain from control methods is very high. Basic research could be encouraged in this area but we ought to think more before we spend large amounts on development.

OPEN DISCUSSION

Hudson: Could Dr. Weidhaas tell us if there is any correlation between the attractiveness of different subjects and the subject's skin temperature?

Weidhaas: I think so. I can at least give you a summary of information derived from Gainesville. It deals with olfactometers and *Aedes aegypti*.

It is relatively easy to identify subjects that are more or less attractive. A series of tests were run with 50 men and 50 women to compare a number of factors such as skin temperature plotted against attractiveness. This showed a gently increasing curve, the higher the skin temperature the more attractive response was gotten. However, in the middle region of the curve there was no significant difference. There were significant differences between the skin temperatures of men and women, men being slightly more attractive than women.

Lactic acid was examined in the same way as skin temperature. You can put the amount of lactic acid given off by a subject on one axis and attraction on the other. You get a curve which shows you some degree of correlation and it seems to hold up. But if you look at individuals it's mighty complex, and one individual may show you this kind of phenomenon while another may not. So I think that what we are really looking at is a complex system of interrelated factors.

Dr. McClelland mentioned that repellents have no effect on tabanids. I would say they do have some, but they are not completely satisfactory, perhaps Dr. Hocking's hat and some clothing would do as good a job as any.

Attractant traps were also mentioned. I think the idea is good, and I think that either you divert some from humans by other attractants or you try to attract the insects to some area and actually kill them. Eventually, perhaps you could have some effect on density.

I think, in general, the attractants we have are not potent enough to do this job so that people are really protected.

Coffey: I wonder would the panel care to say a word on the subject of repellers, perhaps addressing themselves to that very interesting model we heard of, the aluminum foil white hat, and also the one I mentioned, the dragon-fly on the string. I wonder if in the first case we are dealing with a portion of the energy spectrum which has some effect on biting flies but which has not been examined carefully. In the second case, is it possible that predators do emit frequencies which, if properly reproduced and analysed, could be used instead of repellents? These might replace the attempts at sonic repellers, which I understand have not been successful. I do make the point that it is possible today in the sonics area to reproduce in a very sophisticated way all the components of any sort of a noise signature and here you may be dealing with a chord or a very elegant series of frequencies, rather than the single one that has been used on the sonic devices to date.

DeFoliart: If I remember correctly, the aluminum hat was attractive to blackflies. The hat was covered with fuel oil; insects would come in (attracted by the hat) and become stuck in the oil. This relates to an earlier point made that you can offer something attractive which diverts the insect from the part you want to protect. Also, on the subject of the hat, when aluminum was replaced by an olive drab it caught no flies. Therefore, aluminum itself, maybe its reflectance, may have something to do with it.

Downes: It is established that for a number of biting flies, particularly blackflies and tabanids, there is a visual component in their host seeking and landing behaviour. For instance, Dr. Fallis' group have shown that the precise site of landing of a simuliid on a loon depends on the shape of the loon and the pattern of the neck.

With regard to the dragon-fly, I do not think it is impossible. Whether the stimulus that the hovering dragon-fly puts out is auditory or visual in regard to the incoming mosquito, I couldn't guess at all for the moment, either is possible. Of course, I think the whole incident needs to be rechecked. I have observed *Aedes vexans* swarms being preyed upon by a ceratopogonid predator. The *Aedes vexans* runs back and forth in its swarming flight, with the ceratopogonid predator hovering like a sparrow-hawk within the swarm. Suddenly it changes its flight mode, when by chance one of the swarming potential prey come within about a couple of inches of it. It lands on the prey, pierces it and sucks the juices. But *Aedes vexans* can perceive the danger and take avoiding action, it suddenly suspends its back and forth flight and swishes around the predator. So I am not inclined to disbelieve the dragon-fly story, I think it's interesting.

DeFoliart: I think similar activity has been observed with hovering tabanids. When predatory wasps come in the tabanids scatter, whether they see them or hear them is not known.

Mulla: I think Dr. McClelland brought out some very good points regarding specific methodologies such as autocidal control and oviposition attractants. We are aware of the problem of economics and I would like to mention the screw worm fly control program which has been going on in Texas for 10 to 15 years. The cost of the program is far less than the cost of damage done to livestock in Texas.

There are some highly specific oviposition attractants, but these are so specific that if they work on *Culex tarsalis* they will not work on *Culex quinquefasciatus* and vice versa. The question is who is going to put up the money necessary to develop these kinds of compounds.

The other point I would like to make refers to Dr. Sommerman's remark that repellents do not cause environmental pollution. I think she means relatively, because when you use these on a large scale either on animals or on humans, they have to be washed away. Now what happens to these chemicals? They go back into the water systems, into the soil and into the air. So we are back to the pollution problem, but the effect of repellents probably would not be as severe as that of larvicides and adulticides applied to large breeding areas.

I would like to comment also on the use of ultra-frequency sound in repelling mosquitoes. Very recently an engineering firm in California distributed a device producing some kind of distress sound which they claim repels mosquitoes and other biting flies. I have not tested this unit yet.

Cooper: After listening to the program throughout the week, I would like to refer briefly to Dr. Brust's paper and bring up one or two points that I think are important. If we must use chemicals we should pay more attention to the formulations that we are using. As you are aware, many of the formulations for water media are developed to the specifications of WHO and these are at approximately 70°F. Many compounds are brought to Canada and we find that water temperature has a great effect on the emulsification systems which are being used. In many cases I am sure that the poor results that may have been obtained resulted in more chemical being used than necessary simply because the formulation does not suit the situation. We need to work more closely with the new breakthroughs in the emulsification systems which are being developed with surfactants and emulsifiers.

I would like to comment also on the fact that we need more information from the people studying control, on what type of control they wish. Do they wish the compound to stay close to the bottom? Or, do they wish it to be near the surface? In the last year we have shown that some products applied in cold water with various metallic ion concentrations do not act in the way we expect them to, and it depends largely upon what type of water you wish to treat. We need to know more about pH, we need to know more about the metallic ion content and we need to know more about where you want the toxicant to be to give maximum control. This is very important if we are going to reduce the pesticide load that we are currently using, and I hope this phase is not overlooked. If we must use chemicals, let's use them right and use as little as possible.

Downes: I would like to comment on some of Dr. McClelland's observations. Inversions, of course, are decisive indicators of specific distinction only when they occur sympatrically with the standard chromosome and yet no heterozygotes are detected in an adequate sample. In the *Eusimulium aureum* case for instance, seven entities were distinguished, two sympatric chromosomal types in Ontario, two more in the Prairies, a single one in California and two more in Europe, sympatric at least in the area of Leningrad. In each of the three cases where pairs of forms occur together, heterozygotes were not found and it was concluded that the pairs represented good species. Strictly speaking, the method indicates no more than this, but in this particular case there are other persuasive considerations, relating to the method of sex determination and the differing complements of floating inversions, that strongly suggest there are not just three pairs of sibling species but in fact six, or probably seven, distinct types.

Rai: The work of Rothfels and colleagues has demonstrated that there is very extensive inversion polymorphism in blackflies, but, of course, it is not the inversion *per se* which is responsible for reproductive isolation. What happens is that the inversions keep the particular block of genes intact from generation to generation; and in the course of time, the inverted and the normal segments might diverge sufficiently by accumulation of different mutations to be related to or to be responsible for any reproductive isolation that might occur between different populations of blackflies or *Anopheles gambiae* or *Anopheles maculipennis.*

Bellamy: I want to ask about the chromosomal inversions in blackflies. Possibly Dr. Rai has covered the point, but I am not quite clear about it. As I understand it, both the inversion and the standard chromosome can occur in the homozygous condition, but the heterozygous condition may be absent from the population sample. It is assumed, therefore, that the inversion constitutes a complete barrier to the crossing of the two types. But I would suppose an inversion can only be generated singly, and in the next generation would necessarily occur in the heterozygous condition and would thus be eliminated at once. I do not see how the isolated population carrying the inversion in the homozygous condition could be brought into existence.

Downes: As Dr. Rai has explained, and as I should have explained in my talk, it is not the inversion as such that constitutes the incompatibility. Rather the inversion, being a region of the chromosome in which crossing over cannot occur, allows mutations to accumulate within it, perhaps slowly, but perhaps also rather rapidly, to such an extent that incompatibility is established. The occurrence of the inversion provides the substrate for sympatric speciation, rather than the act of speciation itself. Dunbar (1965) has discussed this question.

Rai: Dr. McClelland raised the point that methods of genetic control might not be either practically or economically applicable where there is a vast expanse of land and a great deal of diversity in populations. I quite agree. However, I am quite certain that there is not very much work being done in Canada on the genetics of biting flies. I think that the investment of funds to start investigations on at least a few important species would be very appropriate.

Service: Dr. Bay spoke briefly about density factors. With *Aedes cantans* we have noticed that when there is a very high larval population this usually results in a high adult population, but adults are always small and we find they lay relatively few eggs. In another year when the larval population is smaller, there will be fewer adults, but they will be bigger and lay more eggs.

Weidhaas: Again speaking of our experiment on Seahorse Key, we did see density-dependent factors come into play with the population under control by sterile male releases. We saw no change in reproductive success during the first generation. In the second generation the reproductive success of this population increased to fivefold; 3 to 4 weeks after starting, and in the next 2-week period, it increased to tenfold, 5 to 6 weeks after starting. It took 6 weeks before the changes became really apparent.

We did some release experiments on the island with female *Culex quinquefasciatus* tagged with P 32. We could identify the rafts by their radioactive content, and by plotting the time of collection of the egg raft with the time of release we could determine the gonotrophic cycles. Generally they were about 3 to 4 days, but in some cases we had some evidence that first egg rafts were still being laid after 12 days.

Whitehead: It seems to me that the problem we have in taxonomy is that taxonomists present a picture of fairly discrete entities. If you have 10 or 15 species you would expect to find very serious taxonomic problems amongst them of the sort mentioned by Mr. Downes. The only instance in which one would not expect to find such problems would be with single populations or essentially panmictic groups of populations.

I think the practical entomologist would like clearly described analyses of the pattern of geographic variation, so that from the results of an attempted control of one population he could predict effects of similar attempts at control on other populations.

Service: Andy McClelland remarked on *Aedes cantans* biting during the day in sheltered situations and wondered if this was really opportunistic feeding or did it reflect advancement of the biting cycle because of the dark situations provided by the vegetation.

In reply, I do not think this was so because the light intensity within the sheltering vegetation in the wood and outside it was not very different. The bait catches were made in the wood during the day and the initial high biting population peters out after 15 to 20 minutes. This indicates to me that we were merely sampling the local population.

Finally, with respect to the possibility of facultative autogeny in *Aedes cantans*. Our observations are that if you give unfed *A. cantans* females sugar solution they will live from 7 to 9 weeks in the laboratory, but will never develop their ovaries on this. In addition to this, adults coming to the bait at the beginning of the biting season are all nulliparous.

In marked contrast, adults of *Mansonia richiardii* which came to bait were all parous and we attributed this to first-cycle autogeny.

Downes: Dr. McClelland also referred to the question of autogeny as promoting inbreeding and perhaps therefore tending to promote speciation. He was inclined to object, if I took him correctly, that outcrossing is essential for survival. Outcrossing is surely the normal mode of long-term species survival and evolution, but I do not think it is the only adaptive breeding system for all species. Botanists, for instance, are familiar with many kinds and degrees of limitation of outcrossing, often culminating in apomixis in weedy species and in the Arctic. And even if it is not conducive to long-term survival, we do not know that these autogenous species are in fact all long-lived entities. I think the indications are that they are not long lived as compared with the blood-meal-dependent forms. The family Simuliidae has gone on through the ages, perhaps from the early Cretaceous, as a predominantly bloodsucking group. The autogenous species, I suspect, come and go, conceivably as Bob Peterson was hinting even within a few seasons, but very likely within a million or so years of their generation: there is no reason to suppose they are usually long-lived forms able to survive a succession of major environmental changes. In regard to blackflies, I feel sure that outcrossing is not always the adaptive mode. On the Arctic tundra most species are autogenous and thereby tend somewhat to inbreeding. I examined some ten species and found that several of these autogenous and thus somewhat non-dispersing forms have also lost the swarming flight and mate immediately beside the stream at the point of emergence. This must set up an even greater tendency to inbreeding. Three of the ten species, finally, are maleless parthenogenetic forms in which all possibility of gene exchange has been lost. Only one other parthenogenetic blackfly is known. It seems clear that a progressive limitation of outcrossing must have some important adaptive value under tundra conditions.

Service: Dr. Hocking asked, "From which direction out of the blue does *Aedes cantans* arrive in relation to wind, topography, etc., for feeding on man? "

In the wood, where the catch was made wind speed was very low indeed and the topography seemed to be the same all around. However, I have noticed that when you sit with your legs stretched out in front of you, you very often catch more on one leg than on the other.

Corbet: On the subject of which way mosquitoes arrive. I did a biting periodicity study on my own in the Arctic once and I collected the mosquitoes as they arrived at the bait, which was myself. At the wind speeds that could be measured with the instruments I had available, they always arrived upwind. At very low wind speeds it appeared that they were still arriving in relation to the wind and therefore always arrived from a single direction.

DeFoliart: Can anyone explain why they arrive in pulsations?

Corbet: I think Dr. Service mentioned a possible explanation of this, that one was exhausting the immediate area within which the bait was attractive.

Service: I have noticed both in Africa and England that mosquitoes do not arrive regularly at the bait, there may be an interval of several seconds, or a minute, with nothing and then 3 or 4 will come, almost simultaneously. I have observed this repeatedly but I don't know why it is. It could be that at very low wind speeds small unappreciable changes alter the odour stream and stimulate a group to come down together.

Pučat: From some landing rate studies I have done with *Culicoides* I believe that the biting rate depends on the population density. If the population is high, they attack in great numbers from the beginning of the observation period of a half hour, with the highest peak of attack occurring in the first six minutes and smaller peaks following approximately ten and twenty minutes later. If the population is low they start slowly and build up gradually, with the first peak occurring after 15 minutes of observation.

Provost: We must be very careful to distinguish between an odour stream from the bait going out and reaching the insect and pulling it in, and spontaneous flight.

We have established our species as being crepuscular or nocturnal, or diurnal. The great majority are crepuscular with a certain level of activity during the night and none whatever during the daytime and vice versa. You can go into areas where nocturnal species are resting during the daytime and get bitten, but you have to remember that the insects are not spontaneously looking for an odour stream. You bring your odour to them and this situation often exists in the course of taking biting counts. I think that what you are really doing is not sampling the population, but measuring the adequacy of where you happen to stop as a daytime resting place for nocturnal mosquitoes.

SUMMARY

Rapporteur . . . . **Susan McIver**

In this presentation I will summarize briefly the papers which were given this morning and the comments of the discussants, point out two specific recommendations which emerged from today's deliberations, and indicate four general considerations which underlie, not only what has been said today, but the entire symposium.

In Dr. Weidhaas's paper on personal protection he stated that due to a variety of reasons the use of protective clothing and repellents is the only means available for protection against biting flies in many regions of the world. Of the 10 to 20 thousand compounds screened for use as topical or individual repellent, DEET has proved to be the most outstanding. However, no known repellent, including DEET, is entirely satisfactory. The loss of protection by repellents appears to be correlated with the rate of loss from the skin due to abrasion, evaporation, and absorption. Dr. Weidhaas also mentioned that at present no effective systemic repellent is available. He stated that wide mesh netting which has been treated with repellents offers much promise for use as bednets, jackets, and coverings for openings of enclosures.

The basic point emerging from Dr. Weidhaas's paper is that partially effective repellents, such as DEET, are available but that for the development of more effective repellents the following lines of endeavor must be pursued: (1) There must be continued investigations into the mode of action of repellents and continual screening of compounds for repellency. (2) There should be extensive studies, both physiological and morphological, into the receptor mechanisms used by the insects for the perception of the repellent. (3) Studies on the attraction of biting flies to their hosts should be encouraged. These investigations should involve a search for the attractive stimuli, the specific stage or stages in the host-finding process at which they act, and the distances at which these various stimuli are effective. (4) Work on additives which slow down the rate of loss and formulation of repellents would add to the usefulness of known repellent compounds.

Next came a thought-provoking and stimulating paper by Mr. Downes, in which he challenged us to take a closer and more critical look at the species concept as related to biting flies. He encouraged the use of the full array of tools at our disposal including genetics, biochemistry, geography, ecology, physiology, and behavior, as well as traditional morphology. He pointed out that species such as *Prosimulium hirtipes* may turn out to be many species when investigated by some of the newer approaches to systematics. Also he discussed the revolutionary and intriguing possibility of sympatric speciation in black flies. In addition, he mentioned that frequently polymorphism may exist within true biological species. With respect to this intraspecific diversity, he discussed variations found in species with wide geographic distributions. North America provides an excellent location for the study of such distributions, as an almost continuous land mass, extending from the Gulf Coast to the Arctic Ocean, without significant interrupting natural barriers and having a continuum of photoperiodic situations.

In order to plan and execute successful control programs, it is imperative to know precisely the species with which one is dealing, including the diversities which may occur within that species, such as any differing behavior patterns, if and to what extent autogeny occurs, etc. After all, usually it is not the entire species which we are trying to control, but populations thereof, which may be highly diverse. In Mr. Downes' new systematics he urges not only systematists, but the rest of us as well, to recognize the diversity inherent in species and the importance that understanding of this diversity has to doing meaningful basic research and to the success of control programs.

Dr. Service delivered an interesting and lucid account of his studies on anautogenous *Aedes*, particularly *Aedes cantans*, in Britain, and he indicated that the results of his studies may be applicable to Canadian species of *Aedes*. He has studied the entire behavior of the mosquito and not just those activities, such as host-finding, mating, and oviposition, which in the past have been of primary interest to entomologists. His observations and experiments have helped to complete our knowledge of the activities of mosquitoes.

Dr. Service has also made some valuable observations on predation on mosquitoes and the times at which they are most vulnerable. His idea of using the precipitin test to identify the meals of mosquito predators may prove to be a useful tool in the attempt to find and assess the importance of such predators. He indicated the difficulties which can result from using various trapping methods for determining host preferences of mosquitoes.

With regard to the flight behavior of *Aedes cantans*, Dr. Service found that usually this species flies very near the ground, but may fly at higher levels for swarming and mating. Little evidence was obtained from his studies for non-specific flight behavior, and *A. cantans* appears to fly only for dispersal, host-seeking, oviposition, escape from predators, etc., otherwise it seems to spend an inactive life.

For the application of control measures, whether chemical or biological, it is essential to know where the insects are and what they are doing. Through Dr. Service's work much more is now known about the activities of British mosquitoes and his studies can well serve as models for the type of investigations which need to be conducted on our own northern biting flies.

Dr. Brust presented a paper on the distribution of *Aedes* larvae and their control. At present control of temporary pool *Aedes* species is dependent upon the use of short-lived insecticides which are applied by ground crews to heavily infested pools. In a detailed study of the distribution of *Aedes* larvae around Winnipeg, it was revealed, among other things, that:

1. There is a definite association between the abundance of *Aedes* larvae and the proximity of a blood source such as cattle.
2. The repetitive use of pools by the same or different species is a very important factor in identifying larval development sites.
3. Only 3 per cent of the uncultivated land area around Winnipeg was involved in mosquito production.

The conclusion from this paper is very short, but a most significant one. By knowing the exact distribution of a pest species and treating only those infested areas, the amount of insecticide required for satisfactory control can be kept to a minimum.

Dr. DeFoliart initiated the discussion by referring to one of Dr. Corbet's comments yesterday that nothing attracts funds like success, and he suggested that Dr. Brust's work on the *Aedes* larvae around Winnipeg is a good example of a successful control program. The importance of communication, not only among entomologists, but to the public and to the people who control finances, was stressed by Dr. DeFoliart.

Dr. McClelland commented specifically on the four papers presented this morning and made several general statements. I think two of his general statements require special mention. The first of these is that in our deliberations and discussions in the past three days very little has been said about population dynamics, and yet we have been discussing biological control for which population dynamics is the foundation. Dr. McClelland also brought up the point of the practicality and economic feasibility of autocidal control programs in a country such as Canada with its huge land area and many pest species, usually widely dispersed.

Dr. Sommerman, who works in an area quite similar to the northern part of Canada, stressed the necessity of using repellents and protective clothing in such areas. She made the practical suggestion that local facilities for "recharging" clothing, bednets, etc., with repellents should be established. Dr. Sommerman also characterized three biting fly regions in Alaska and discussed the problems which occur in each of them. She mentioned the misuse of insecticides and she recommended better training and control of the individuals who apply insecticides, to encourage reduction of the amount of these agents unnecessarily and unwisely used.

Specific Recommendations

There are two outstanding points which arose from today's proceedings. The first is that due to costs and the impossibility of area control, one must rely on personal protection methods in sparsely inhabited areas, thus including a large percentage of Canadian territory. Continued and accelerated research for better repellents and protective clothing is recommended.

Secondly, the exact spatial and temporal distribution of the target or pest species should be determined in planning control programs, in order to keep the amount of insecticide required to a minimum. Not only is this recommendation in keeping with the preservation of environmental quality, but it has economic implications in calculating the amount of financial outlay necessary for control programs.

General Considerations

When considering a control program, four superficially simple questions need to be asked about the pest species.

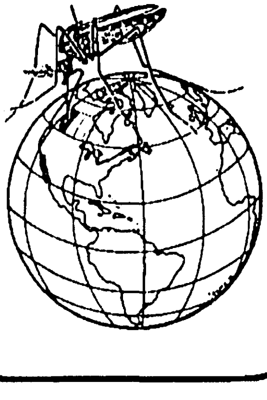
1. *What is it?* With what species, subspecies, and population is one dealing?
2. *Where is it?* What is the temporal and spatial distribution of the species?
3. *What is it doing?* What is the behavior of the species?
4. *How does it accomplish the observed behavior?* What are the underlying mechanisms of behavior?

The success of any control program, be it chemical or biological, rests directly upon the depth, sophistication, and subtlety with which we can answer these questions. Yes, we have made progress in being able to provide answers to these questions and the participants of this symposium have certainly done their share, but we still have a long way to go before the answers are complete.

A quotation from Robert Frost's well-known poem seems a most appropriate way to close this discussion.

> The woods are lovely, dark and deep,
> But I have promises to keep,
> And miles to go before I sleep,
> And miles to go before I sleep.

Resolutions



RESOLUTIONS COMMITTEE

**Corbet, P. S	Chairman, Department of Biology, University of Waterloo
*Fettes, J. J.	Chemical Control Research Institute, Department of Environment
*Lindsay, I.	Secretary of the Advisory Committee on Entomological Research to the Defence Research Board
McIver, Susan	Department of Parasitology, University of Toronto
*Hocking, B.	Chairman, Department of Entomology, University of Alberta
*Hudson, Anne	Chairman of the Organizing Committee, Biting-fly Symposium

Invited to Attend:

Haufe, W.	Veterinary–Medical Entomology Section, CDA Lethbridge

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*Members of the Advisory Committee on Entomological Research to the Defence Research Board

**Chairman of the Advisory Committee on Entomological Research to the Defence Research Board

INTRODUCTION

P.S. Corbet
University of Waterloo

"The purpose of this exercise is to take advantage of the fact that we are all here, we are all interested in the same kinds of problems, and we have just heard three days of deliberation on the subject. While these are still fresh in our minds, it seems useful to try to crystallize some of our ideas in statements that we can support, and particularly for the Committee on Entomological Research to the Defence Research Board and the Canada Department of Agriculture. We hope that the resolutions that come out of these meetings can help decision-makers and therefore, indirectly ourselves as practitioners of Biting-fly Research. We hope that these resolutions will not be allowed to restrict the scope for new ideas or restrict any support for other areas that may emerge in the future. In brief, we hope they will not be regarded as comprehensive or restrictive.

It follows from this, we hope, that any one statement that can receive majority support by a group of this composition is better than no such statement. Thus, I do not think we are interested at all in the narrow passage of a controversial resolution; we are interested in something that virtually all of us can support. I think that for such an exercise to be successful, where all hold such varying views, we must practice the art of compromise, on the grounds that the more general you make a resolution, the more people can agree with it, but the less use it is. I suggest that we may find it helpful to guide ourselves in this exercise by giving prior consideration to the needs of Biting-fly Research in Canada, regardless of our own individual situation or interest, and by giving greater attention in the resolutions to their intent than to the details of working, unless we consider the existing wording is misleading or incorrect. A possibility that we might keep in mind is that the Resolutions Committee would be empowered to make minor modifications of style or rectitude in the wording if the group agreed to this."

Following the discussion of each resolution and the incorporation of amendments, a motion to accept the resolutions was passed *nemo contra* with 78 in favour, none against and 5 abstentions.

Resolution Number One

WHEREAS mosquitoes, blackflies, and deerflies and other biting-flies have a substantial socio-economic impact on:

- the health and welfare of man and domestic animals
- military efficiency
- industrial and agricultural production
- the management of resources
- the future of northern and wilderness regions

AND WHEREAS insufficient socio-economic information is available, and a sound strategy for biting-fly control with distinct criteria for the assessment of success does not exist

BE IT RESOLVED THAT planning in science and technology be directed to:

1. A definition of the problem and criteria for control;
2. The development of strategies for biting-fly control and research, emphasizing systems analyses and socio-economic assessments.

Resolution Number Two

WHEREAS at present synthetic chemical pesticides will continue to play a major role in the repression of biting-fly populations

AND WHEREAS there is a vital need to reduce the amount of such pesticides applied to the environment

AND WHEREAS research and development of alternative methods to synthetic chemical pesticides have progressed and much has been done to advance the technologies of biological, autocidal, genetic and mechanical methods of control

AND WHEREAS the demonstration of a success in the use of alternative methods will do much to generate additional support

BE IT RESOLVED THAT priorities be identified and increased resources be devoted to:

- the development, formulation and application of ecologically acceptable chemical control agents
- the monitoring of side effects and the assessment of efficiency
- the development of control methods that offer alternatives to pesticides, particularly those which hold the greatest promise of early application and adoption, e.g., pathogenic organisms (especially mermithids); application of juvenile hormone analogues, genetic manipulation, and to monitoring and assessment of these methods
- the development of integrated pest management programmes
- the improvement of techniques for *in-vivo* or *in-vitro* propagation

Resolution Number Three

WHEREAS the effectiveness of all control operations depends on their suitability for the species and stage of that species against which they are directed

AND WHEREAS biting-fly populations are influenced by populations of the host and other species with which biting-flies interact

BE IT RESOLVED THAT resources be directed towards a mission-oriented basic ecological study of biting-flies consisting of the contributory studies of:

- basic biology
- speciation and variability
- distribution in time and space
- detailed life cycles
- relationships with other organisms
- behaviour
- physiology

Resolution Number Four

WHEREAS in many regions and situations area control of biting-flies may remain inadequate or unfeasible

BE IT RESOLVED THAT immediate attention be given to improvements of methods of personal protection such as repellents, protective clothing, tents and other shelter, and a psychological approach to the problems of over-reaction to biting-flies and to the promotion of a more tolerant attitude towards them.

Resolution Number Five

WHEREAS the layman's understanding of the biting-fly problem is inadequate

BE IT RESOLVED THAT increased effort be given to the improvement of the quality and quantity of communication and publicity between the scientist and the media, the public and governments, in order to:

- ensure that the complexity of the problems of controlling biting-flies is understood
- prevent the results of research and development on biting-fly control from being presented in a misleading or erroneous way
- ensure that all educational levels are kept informed of biting-fly problems and progress
- increase the understanding of the representatives of other scientific disciplines, particularly relevant physical scientists, of the problems in biting-fly control.

End of Resolutions

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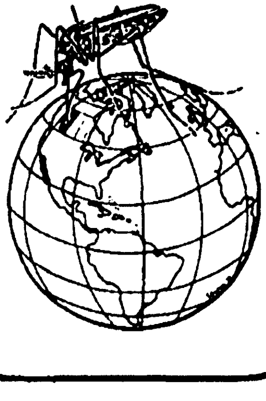

SUBJECT INDEX

SPECIES INDEX