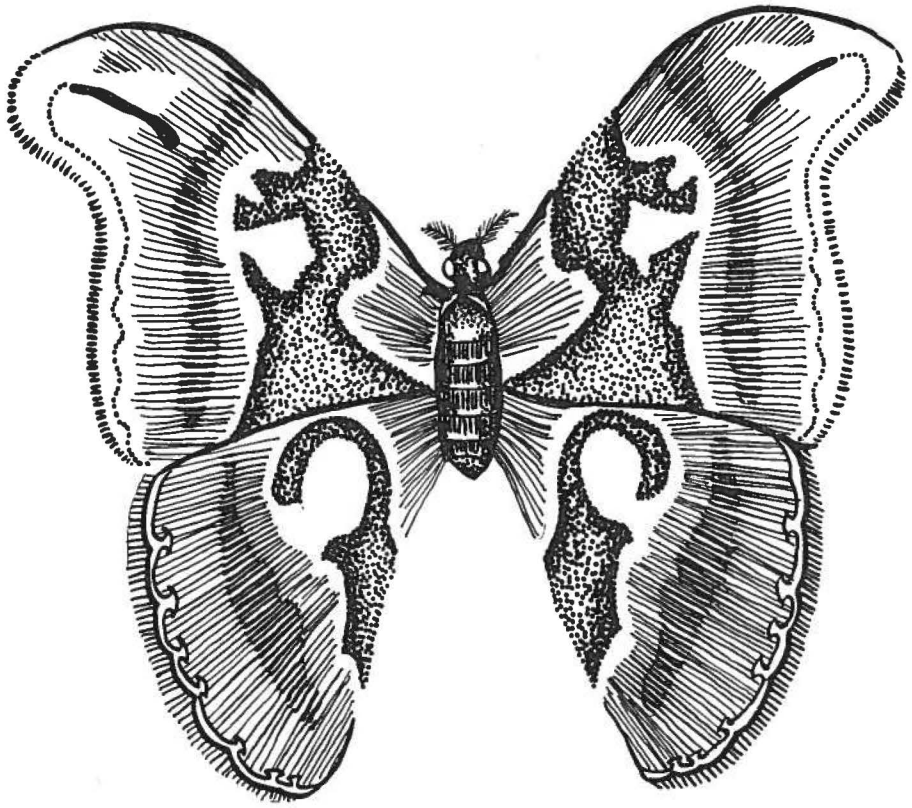
VOLUME 4 1970

J. E. Guthrie



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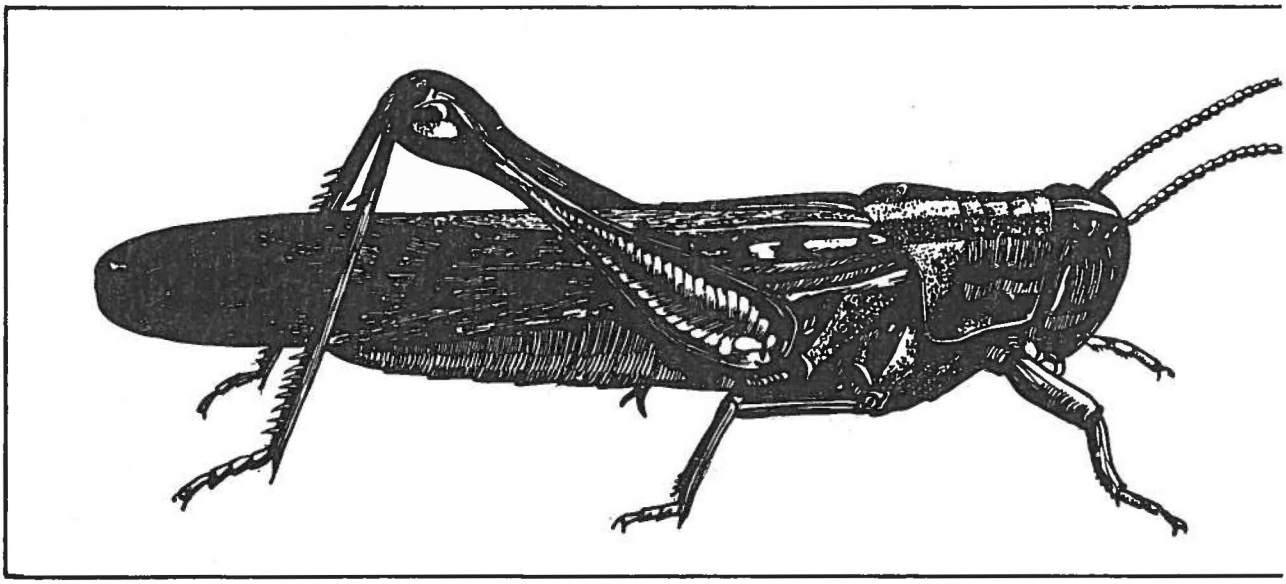

THE MANITOBA ENTOMOLOGIST

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1970

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THE MANITOBA ENTOMOLOGIST

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THE MANITOBA ENTOMOLOGIST

An official publication of the Entomological Society of Manitoba, an organization to foster the advancement, exchange and dissemination of entomological knowledge

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RADIATION INDUCED MUTATIONS IN INSECTS

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Contribution to a symposium on "Ionizing Radiation in Entomology" at the Joint Annual Meeting of the Entomological Society of Canada and the Entomological Society of Manitoba held at Winnipeg on August 24-26, 1970

ABSTRACT

Ionizing radiation is usually employed as a tool in entomology, either for tracer or tagging studies or for the sterilization of males and females for control. On the other hand insects themselves have long been employed as experimental animals in quantitative research on the mutagenic effects of radiation. These studies established several classical principles in radiogenetics that have now been applied to man. One of these is that the induced mutation frequency varies linearly with dose and is independent of the intensity at which a given dose is administered. Recently an intensity effect has been found in studies with mice, indicating that a proportion of pre-mutational changes are capable of repair during chronic irradiations. The present paper describes how the chalcid *Dahlbominus* has been employed in studies of mutation frequency, with particular reference to the relative effects of acute and chronic exposures on eye colour mutation frequency, and to the presence or absence of a threshold effect at lower doses (i.e. some level below which no mutations are induced). The implications of the results with reference to radiation protection are discussed.

In the papers presented today in this symposium, the authors have discussed the results from studies in which radiation or radioisotopes have been used to implement programs on the ecology or the control of insects. As the last speaker, it is my intention to discuss some aspects of the use of an insect as a biological indicator of the effects of radiation on cells, with special regard to the interpretation of the genetical hazards inherent in irradiated populations. For this purpose, I will describe the development of a problem on mutations in the wasp *Dahlbominus fuscipennis* (Zett).

In introducing the general subject, we should perhaps consider the possible effects of radiation-induced mutations in human populations. Mutations affecting man are extremely diverse, ranging in effect from harmless mutants such as hair or eye colour changes to serious hereditary diseases such as achrondroplasia or hare-lip. For convenience, these mutants can be grouped as lethal, harmful, minor and beneficial (James, 1963). Of these four, the group producing harmful hereditary diseases and handicaps is of first importance in terms of damage. All of these mutants are already present in populations, and the effect of radiation is not to produce new mutants but to produce more. It has been estimated that in the present human population, at least 4% of all individuals born suffer during their lifetimes from a disabling hereditary condition, and mutations induced by radiation contribute substantially to this load of defects.

In the history of research on the hazards of radiation, early estimates were derived solely from mutation frequencies found in irradiated *Drosophila*, and many of the basic principles of radiogenetics came from studies with this and other lower animals. One of these principles, from work on *Drosophila* spermatogonia (Muller 1954) was that mutation frequency (recessive lethals) is dependent solely on the dose of radiation, no

matter what the intensity (or dose rate) at which it is administered. This principle has been related to the concept that mutation is caused by a single hit resulting in a linear dose-effect relationship. Recently, the *Drosophila* results have been challenged by work with mice, and Russell (1965) has found that in comparison to chronic irradiations, acute exposures will result in four or five times higher frequencies of coat pattern mutations. Thus, Russell has formulated a hypothesis that some step in the mutation process may be capable of repair or recovery. The mouse data also showed that mutation in these animals is at least 15 times higher than in *Drosophila*, indicative that the hazard of mutants in human populations may be higher than former estimates. Such differences would have very important implications in the evaluation of genetic risks from radiation.

Our work with *Dahlbominus* has been designed to compare the effects of acute and chronic exposures on eye colour mutation frequency and to test for the possibility of a deviation from a linear response.

Material and Methods

The insect *D. fuscipennis* is a small cocoon parasite of sawflies, reared in our laboratory on over-wintering cocoons of *Neodiprion lecontei* (Fitch). *Dahlbominus* provides several technical advantages for the study of the effects of radiation on mutation for instance, four clearly visible eye colour mutants appear at high frequencies among progeny of irradiated females (Baldwin *et al.* 1964). These colours, named carmine, claret, chestnut, and russet, can be easily seen under a binocular microscope, in contrast to the blackish-brown eyes of the wild phenotype. The genetics of these mutations has been studied (Baldwin *et al.* 1966), and it is known that the colours occur at a minimum of 8 loci; mutation at a single locus can produce as many as three different eye colours. Crosses have shown the presence of two linkage groups and two allelic series of three alleles each. In *Dahlbominus*, unfertilized diploid females produce eggs which develop into haploid males, and all mutations will appear among the first generation sons. This feature eliminates the necessity for tedious back crosses which are usually required to detect recessive mutations. The identification of the two sexes is readily done in the pupal stage by body size and by antennal length, making it possible to eliminate males before the females emerge as adults. The short period of time required for development from egg to adult (16 days) and the large number of eggs (10 to 40 per cocoon) make it possible to obtain large numbers of progeny in a short period of time. Conveniently, *Dahlbominus* can be stored for long periods of time at low temperatures, a feature which facilitates genetic studies involving test crosses.

The irradiation of the experimental material was done with a Gammabeam 150 (Commercial Products, AECL, Ottawa) and a small 75 mCi Co^{60} source in our laboratory. Acute exposures (with the Gammabeam) were completed at 100 R/min in all cases; chronic irradiations with the small source usually extended over 4 days (100 hours) and the dose rate was adjusted to give the appropriate total exposures in this period of time.

Mutation Sensitivity

A very difficult problem in experimentation with most animals arises from the fact that sensitivity to radiation-induced mutation varies with the stage of development. For example, Purdom and McSheeley (1963) have stated that the various stages of spermatogenisis in *Drosophila* vary considerably in their sensitivity, as comparable sampling from successive stages of the development of the fly is impossible when different stages are used. Tazima *et al.* (1961) has shown that early and late gonial stages of the silkworm show completely opposite mutation frequency effects with acute and chronic exposures.

In early work with *Dahlbominus*, in which the insects were irradiated as early and late larvae, the germ plasm would be in the oogonial stage, and comparable sensitivities were

found throughout this period of development (Fig. I). However, the sensitivity to the induction of eye colours was low in oogonia, increasing rapidly, as shown in Fig. I, from pupae to adults of four days of age (Baldwin, 1965). Since we wished to work at the highest point in mutation sensitivity, a series of experiments to determine the most sensitive stage and to find a period when the sensitivity would remain constant over at least 100 hours (for chronic exposures) was undertaken.

The increase in sensitivity to mutation was clearly a function of the stage of the germ plasm in females, (Baldwin 1968). In a test designed to illustrate this phenomenon, four-day-old females irradiated at 1000 R and placed on new cocoons each day for four successive days produced males which showed high sensitivity on the first day and a remarkable drop in mutation sensitivity on succeeding days (Fig. II). Thus the highest number of mutants were found in these females on the first day of oviposition; by the fourth day, the frequencies had dropped to levels comparable to those found when irradiations were done at the larval stage, indicating that only oogonia remained after four days. To overcome the difficulty of falling sensitivity, females in all experiments were killed after the first 24 hours of oviposition.

The problem of determining a period when a single stage such as the mature oocyte stage could be irradiated over several days with chronic exposures was solved by dissecting and counting oocytes in the ovarioles of unmated females during 20 days following emergence. In Fig. III, counts of the average numbers of oocytes from eight females at different ages show that the numbers rise to a plateau at about 5 days; from this point the numbers of oocytes remain comparatively constant to about 10 days of age when the numbers begin to decrease gradually, presumably the result of the re-absorption of old oocytes (Baldwin 1968). From this data it was possible to predict that the numbers of highly mutable oocytes would remain constant over a long period of time, and that the sensitivity to mutation might also be constant from 9 to 13 days of age.

Tests of the mutation frequency (Baldwin 1968) from 7 days to 13 days (Fig. IV) proved that a plateau in mutagenicity did in fact exist during this period. Thus, our tests of chronic doses in which the exposure was spread over a 100-hour period from 9 to 13 days could be compared to acute doses administered at any one of the acute irradiations at 9, 11 or 13 days. In practice, the acute irradiations were done at 11 days, or at the mid point of the chronic irradiation times.

Acute and Chronic Irradiations

The effects of acute and chronic exposures were compared at two different dose levels viz., 250 and 500 R. The acute doses were given at 100 R/min at 11 days after emergence; chronic exposures were done at the proper intensities to give the two different total doses over a period of 100 hours, or from 9 to 13 days of age (see caption Fig. V). At both exposures, the results of chronic exposures were higher than the acute data, indicating that repair had not occurred at the slow chronic rates. At 500 R the confidence limits do not overlap, indicating that the differences between treatments may be real. At the lowest doses (250 R) the levels are almost identical. Thus it is improbable that exposures at even lower levels would show any difference with chronic treatments.

These results show that repair did not occur with chronic doses, and that an almost exact linear relationship exists between values at 0, 250, and 500 R. This linearity has been corroborated by current work (to be published elsewhere), in which the acute exposures have been extended to the low level of 15 R.

Discussion

It is clear that eye colour mutation frequency in *Dahlbominus* is dependent on both dose and stage of development, and that mature oocytes in insects represent the most

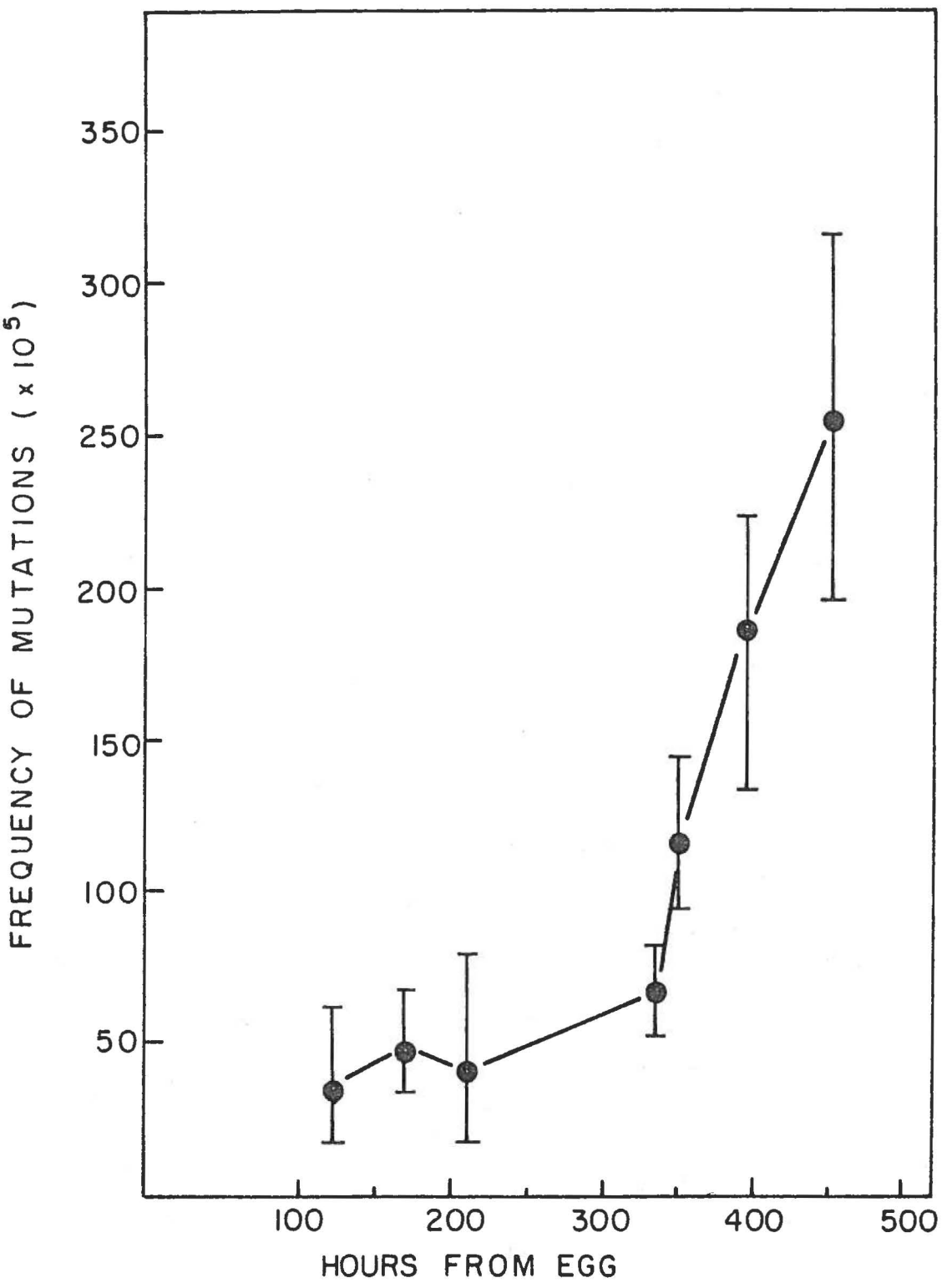

Figure I. Increase in mutation frequency with stage of development in *Dahlbominus* (Baldwin, 1965).

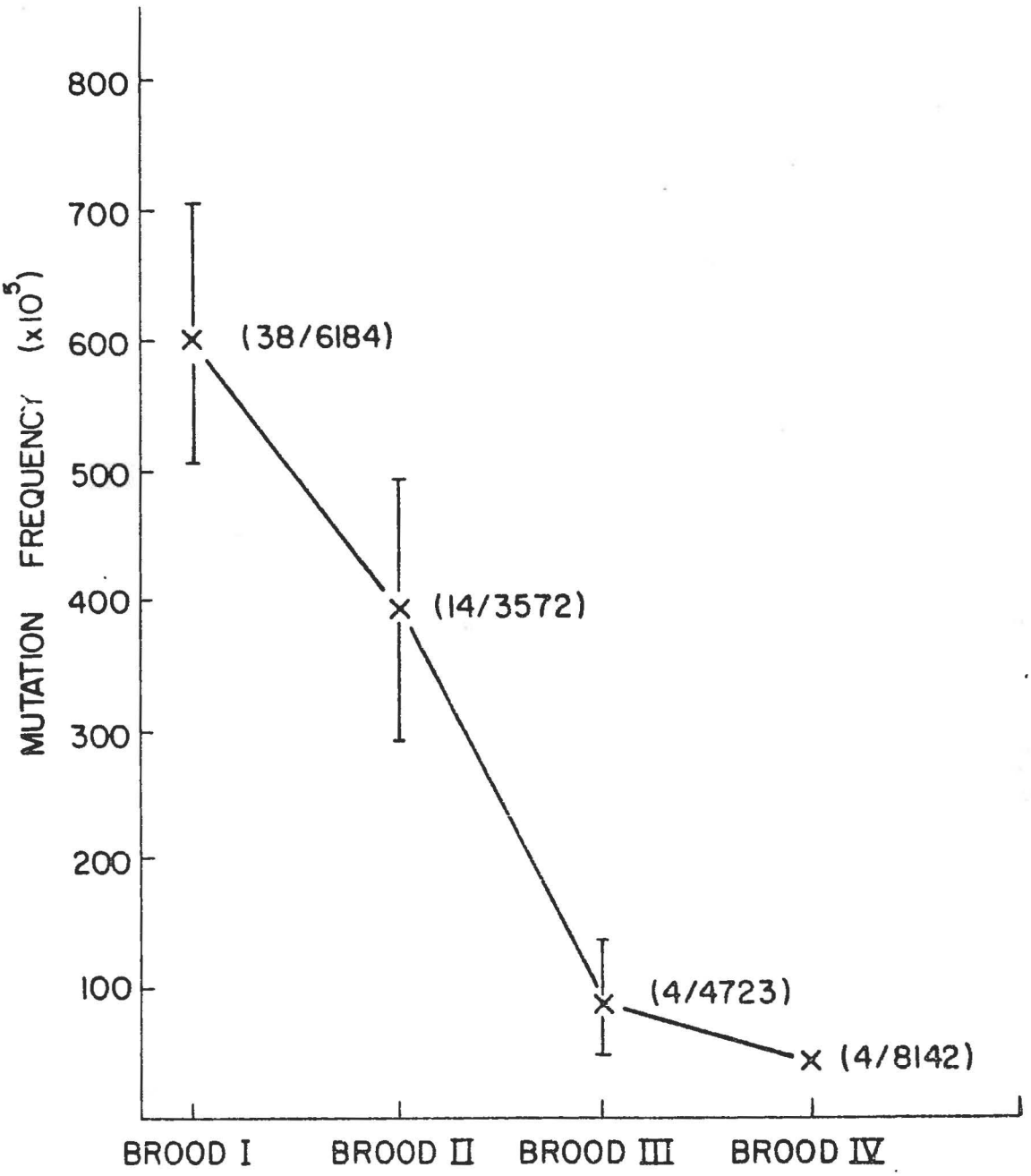

Figure II. Decrease in mutagenesis with increasing age in days in *Dahlbominus* females (Baldwin, 1968).

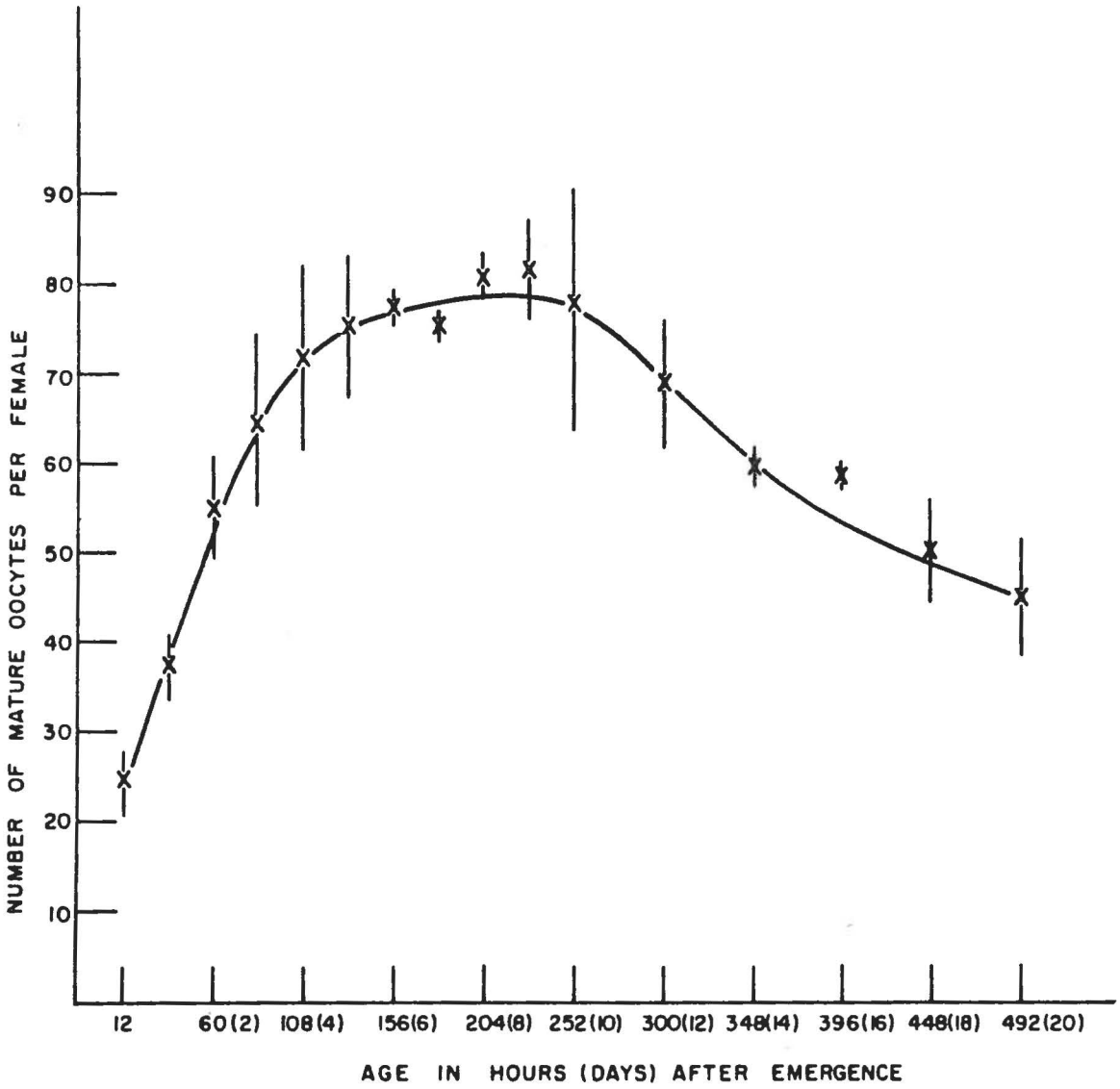

Figure III. Numbers of mature oocytes in aging females with plateau at 6 to 10 days. (Baldwin, 1968).

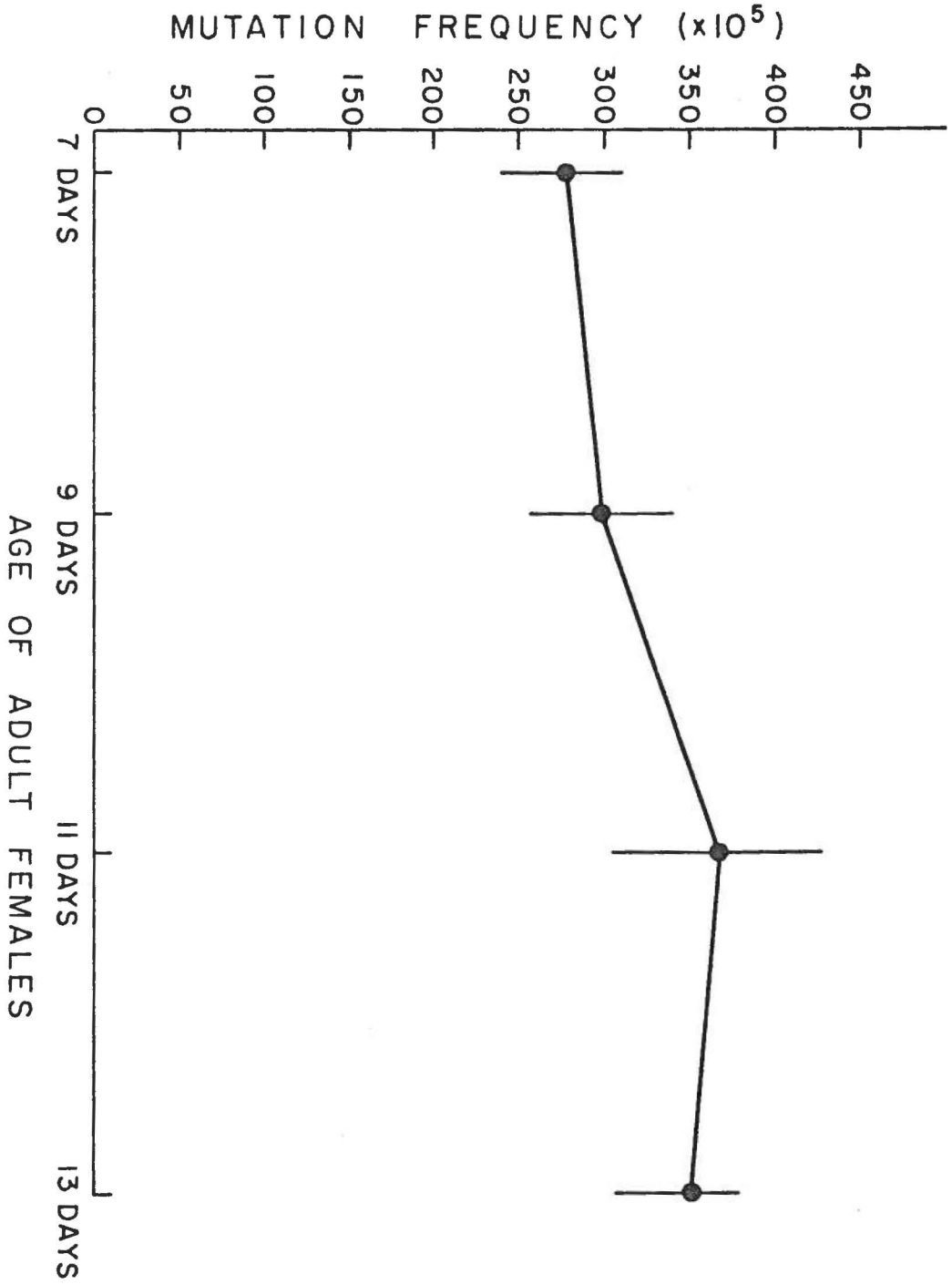

Figure IV. Mutation frequencies following exposure of females at different ages at 500 R (Baldwin, 1968).

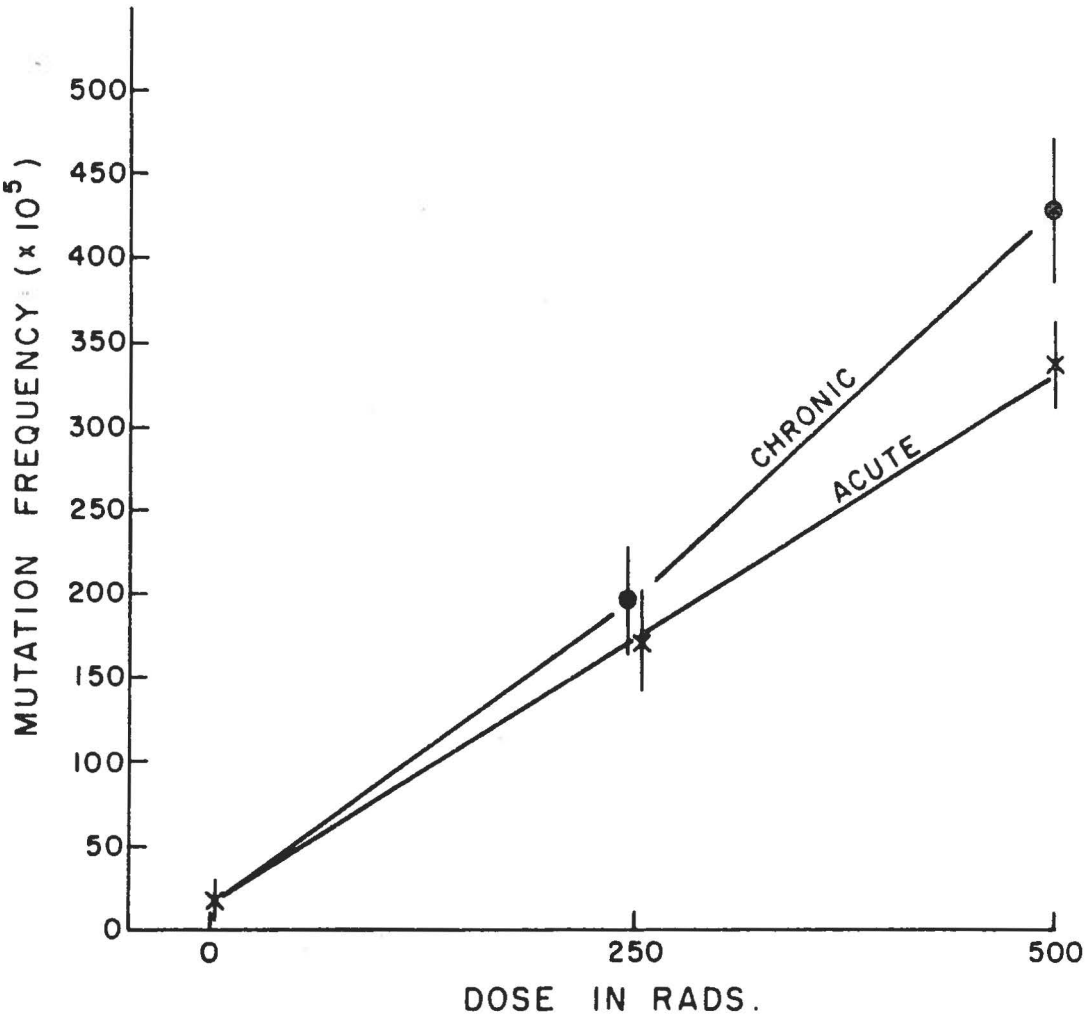

Figure V. Mutation frequencies in *Dahlbominus* after acute and chronic irradiations at 500, 250 and 0 R. (Baldwin, 1968).

sensitive stage in oogenesis. The difficulty of variable sensitivity with age was overcome in *Dahlbominus* by holding the females until 9 to 13 days of adult life, when only mature oocytes were present in the ovarioles. All insects were finally propagated at 13 days and killed 24 hours later. Thus, our experiments were done with highly sensitive oocytes when sensitivity was not variable, a situation comparable to mice, where the germ plasm remains in the dictyate oocyte stage from birth to ovulation.

In *Dahlbominus*, chronic doses administered at rates at least 1000 times slower than the acute exposures gave frequencies which were equal to or greater than those following acute irradiations. Thus premutational repair such as Russell postulates for mice, did not occur in this insect. The same conclusion was reached by Purdom and McSheeley (1963) in studies on recessive lethals in *Drosophila*. Again, Oster (1964) states that despite large scale work, there is still no clear basis for a dose rate effect in the production of point changes in immature female germ cells of *Drosophila*. Also, the apparent linearity between the points at 0, 250, and 500 R indicate that the effect of radiation in producing mutations begins at zero dose, with no threshold at lower levels. This conclusion has been supported by data to be published.

One other point should be mentioned in connection with the estimation of mutation rates in insects and mice. The mouse rates have been calculated at 22.1×10^{-8}/R/locus, as compared with 1.52×10^{-8}/R/locus in *Drosophila*. This discrepancy indicates that mice might be 5 times more sensitive than insects Wolff (1967) leading to the fear that man might be far more sensitive to genetic hazards than indicated by the *Drosophila* figures. It is noteworthy that on the basis of 8 loci for the eye colour mutants in *Dahlbominus* Baldwin *et al.* (1966), the mutation rate in this insect appears to be 90×10^{-8}/R/locus, almost five times the frequency found in mice.

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WHITHER CANADIAN SCIENCE OR WITHER CANADIAN SCIENCE - A CHOICE

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Contribution to a symposium on "Ionizing Radiation in Entomology" at the Joint Annual Meeting of the Entomological Society of Canada and the Entomological Society of Manitoba held at Winnipeg on August 24-26, 1970

ABSTRACT

Intuitively, most of us are aware that we have not yet produced a viable scientific community in Canada. To do so, we will have to encroach considerably more on the resources of the country. These are apt to be denied unless it becomes apparent to the public that the scientific community is not only interested in its own progress, but also the progress of the country as a whole. While it is now generally acknowledged that science is a necessary ingredient of a progressive society, it is equally true that a simple inoculation with science is not sufficient to produce progress.

These and other homely bits of wisdom are the subject of this paper. The author attempts to analyze the confused environment in which the Canadian scientific community finds itself and to indicate what might be done to spur the required future development.

I must thank you for the invitation to address this Symposium. As a layman I have been forced at least to become familiar with your field of interest, an exercise which I have found both stimulating and rewarding.

In response to this kindness, I decided that the most valuable contribution I could make would be to give you an over-view of the state of scientific development in Canada from the perspective of someone attempting to develop a stable, productive, scientific community in the dynamic economic and political climate in which we find ourselves today. Further, with the full confidence of a complete layman, I would like to give you an indication of what the entomological community looks like as part of this picture. If you find that I have misread you, perhaps you will want to reflect that the major decisions affecting the stability or growth of entomological activity are apt to be made by someone who has even less time than I to educate himself.

It is no secret to this audience that a major debate is in progress, which is attempting to define -

(a) What science should be done
(b) How much science should be done
(c) Where it should be done
(d) Who should pay for it.

Canada is not alone in launching such a debate. Every developed country, including the U.S., is either formally or informally going through the same exercise. It is not easy. Scientists are used to being judged by an absolutely fair and unbiased referee - Nature. They are used to being criticized, stimulated, and directed by their peers. Now, suddenly, they are challenged by a patron who exercises human judgment and one who, by and large, is a layman to the scientific community.

We must first understand the basis of this transition in order to develop an intelligent and proper response.

The last two world wars were undoubtedly responsible for the major growth of technological activity on both sides of the conflict. Under the stimulus of war, every margin of superiority is exploited. We have learned that man's ability to defend himself is largely determined by the quality and quantity of the science and technology that he has at his disposal. More important, in the course of vigorously pursuing science and technology, we have discovered that developments have been brought to the point where they have tremendous importance to the quality of our society. As a result of learning to use the science we pursue, we are able to feed ourselves better, to clothe ourselves better, to house ourselves better, to live in better health, to live longer, to communicate better and to generate leisure time and the capacity to enjoy it. Small wonder that the growth of scientific activity has been not only tolerated but actively stimulated over the past fifty years.

In the particular case of Canada, the technical community has been asked to grow very rapidly. Our population of scientists and engineers has increased from about 90,000 in 1963 to about 160,000 today. With fair certainty one can predict the production of a total population of something like 300,000 by 1978 (1). Our ability to produce Ph.D's in science and engineering has increased from 220 in 1959 to 1300 in 1970, and it is reasonably certain that we will be producing 2000 per annum by 1973 (2).

All of these scientists and technologists have been produced by the academic community. It is therefore not surprising that the scientists we have produced have been strongly influenced by the academic stress on fundamental research. Until very recently there was no problem in this regard because the growth of the academic community itself assimilated most of the scientists produced, i.e. there has been very strong feed-back to the universities. We have only within the last two years reached the point where production of scientists exceeds the demands of university expansion.

With this apparent and growing surfeit of highly trained personnel, the following question is being voiced by those responsible for developing our full potential: "Now that we have learned to produce scientists, how are they to be used to make Canada more productive?". The public is saying, "You have been telling us that it would be rewarding to tax ourselves to produce a strong scientific community - now prove it in terms that are apparent to us".

Because we are a little late in addressing ourselves to these questions, there is a growing atmosphere of apprehension. In our preoccupation with finding an adequate answer, there is a danger that we may overlook the fundamental importance of basic research.

THE RATIONALE OF BASIC RESEARCH

Throughout the world, basic research is an activity which inevitably taxes the public purse. At the level empirically known to be necessary, it requires predominantly public patronage, not private. Even in the U.S., the acknowledged champion of free enterprise, the vast majority of funds channelled into basic science are of public origin. (3). It is therefore necessary to distinguish between the motivation of the person engaged in the activity and that of the public, which is paying for it.

Motivation of the Scientist

The best scientists are motivated by the highest philosophic principles - the search for truth, and the creation of symmetry, understanding, order, and beauty. In short, the motivation is more cultural than utilitarian. Those who constitute the large body of average scientists are driven by the vision, if not its fulfillment.

Motivation of the Public

Society as a whole is intuitively aware that the elevation of its prospects includes the need for cultural development. At present, however, Canadian society does not place a sufficiently high value on culture to justify the necessary level of support for basic research

on purely cultural grounds. For confirmation, one need look no further than federal, provincial, or municipal budgets. They offer only modest support for even those cultural activities which the public can see and hear themselves. It is unlikely that Canadians today would enthusiastically support a cultural activity in which they are denied even an audience level of participation.

Basic research is much too important a national activity to risk justification on cultural grounds. It is equally dangerous to seek support on the basis that it has been the foundation for every major technological advance. There are two things wrong with this approach:

a) The time between basic discovery and utilization, although shrinking, is still generally longer than the politically significant interval.

b) The results of basic research are open to the world. It is not credible to the layman that the nation must participate to profit.

We must therefore address ourselves to the question "Why is basic research important to the Canadian taxpayer today?" There are good answers.

a) If Canada is to tap the world fund of knowledge, it must first establish a credit. At the very least, we need people who can critically read the literature. An appreciation of its implications requires active participation. We are all capable of the mechanics of reading medical journals and texts, but would hesitate to practice medicine on the strength of our reading ability alone.

b) The best vehicle we have yet developed for training scientists is the medium of basic research. Even those destined for a vocation of applied science are taught the scientific method and objective discipline through basic research.

c) Basic research serves to retain a technological window of communication between the world and ourselves; and within our borders, between industry, government, and universities. In the case of applied research and development, communication is inhibited by proprietary considerations. As our society becomes more complex and interdependent, it becomes progressively more important to exploit every channel of communication in the interest of developing effective co-operation.

d) Basic research tells us what Nature will permit. It is easy to waste significant resources on applied projects which have a low probability of success. If we are to make a significant contribution, Canada as a smaller nation, must learn the art of retaining a broad view, while focusing the application of its resources. We Canadians must be prepared to pay proportionately more to define those objectives capable of achievement and worth pursuit, so that we can, with confidence, focus our limited resources on their achievement.

e) There has never been difficulty in marshalling the basic research resources of a country to attack a national crisis. Indeed, had we not had the basic scientific community to call on during the last world war, the outcome would have been tragic. It takes a good twenty years to charge this battery of talent, one cannot afford to wait for a crisis to start the generator. Hopefully, the crises of the future will not be those of defence, but rather those associated with the quality of our society. In either case, both natural and social scientists will be required for their resolution.

An Important Point of Confusion in Canada

That science is a necessary ingredient of a progressive society is accepted as almost axiomatic. It is largely on this basis that the public has been prepared to tax itself to build the existing Canadian scientific community. What is not quite so self-evident is that the simple inoculation of science will not make a society progressive. It is a necessary but not sufficient condition. The growing awareness of the latter has sparked the current debate on science both in Canada and abroad.

One of the major difficulties in rationalizing the need for science arises because the vast majority of Canadians make little distinction between the concept of "factories" and the concept of "industry". Industries produce factories; factories produce products. Factories

are obsolete by the time taken to erect them; industries must produce progressively better factories if they are to survive competition. Factories make little use of scientists, engineers, economists, analysts, lawyers, etc. Industries would die without them. If indeed our primary purpose is to elevate the prospects for our society, one of the conditions that must be met is to elevate the quality of work available to the individual. The ratio of challenging to menial work is much higher in "industry" than in its product, the "factory".

Industries require the entire technological structure of basic research, applied research, development, innovation, and production. As we stand today, we are more a nation of "factories" than "industries." Events have led us to attack the problem of building our industry in a most peculiar way. We have simultaneously developed our capacity to produce scientists at one end of the spectrum and to build and operate factories or branch plants at the other end. Both are essential elements of industry. They are costly and time-consuming capabilities to produce and must somehow be kept intact until we can fill in the remaining elements of applied research, development, and innovation. It is extremely important that both ends of our industrial spectrum recognize that they are part of an incomplete structure, the stability of which may well hinge on the degree to which both are prepared to bend to fill the gap.

Where Should Basic Research Be Carried Out?

Throughout the current debate, there has emerged a temptation to allocate various elements of our technological structure to discrete types of institution. For example, I have heard otherwise responsible individuals putting forth arguments in support of the thesis that basic research should be the exclusive province of the university laboratories; that applied research and development should be done exclusively in private industry so that close association will stimulate innovation and early financial reward; that government should get out of research both basic and applied. I find all such arguments highly dangerous to the health and progress of our country.

Universities, government, and industry all profit by engaging in the basic research activity, and it would be erroneous to specify that any one should be the sole repository of this discipline. Indeed, if we are to take advantage of the communication aspects of basic research it is essential that all of them, in varying degree, be engaged in the activity. What is required is a recognition that Canada's industrial development and its capacity to meet the expanded aspirations of its society are going to depend very strongly on the flexibility with which we are prepared to inject all the various elements of technical activity into all of these institutions.

Basic research must certainly be done in universities. It is the best vehicle we have yet developed for training scientists. However, it is important that the universities recognize (as many already have) that their ability to retain a hard core of academic and intellectual freedom may well depend on the degree to which they are prepared to engage in activities which the public can recognize as being directly pertinent to its welfare. Therefore, I believe that the universities can profitably expand their outlook from that of basic research into the applied areas.

For those who argue that government should get out of research, it is important to remember that in one way or another the scientific community in Canada owes its birth to the National Research Council. Had it not been for the establishment of NRC and its visionary leadership, it is doubtful that our enviable capacity to produce scientists could have been achieved. Good science is good science wherever it is done. It is ridiculous to assume that public funds are less productive in a government laboratory than in a university or industrial laboratory. The quality of the scientist is the paramount consideration. NRC has built a highly respected international reputation of excellence, and has been largely responsible for setting the high standard for science in Canada. I see no reason to destroy

this capacity and every reason to preserve it. The concentration of first rate scientists in government, laboratories insures that new and important fields of work do not go undetected. NRC's position as a federal agency of high reputation opens international doors which are denied both universities and industry. It was through NRC that Canada entered the nuclear energy field. If, as I believe, an important function of basic research is to broaden our outlook, it is essential that the Federal Government's capacity to engage in basic research be kept intact.

The mission-oriented laboratories of the other government agencies need an element of basic research for the same reasons that apply in the case of industrial laboratories. Good management has found that it is easier to get the best people and to use them most productively in an environment where basic research monitors the quality and scientific viability of the applied programs.

Strong recommendations keep emerging that public funds should be channelled to support research capacity in industry to improve the probability of innovation and financial reward (4). I find no difficulty in supporting this view. However, as I indicated earlier, though we have a strong productive capacity we have rather few industries. Until our industrial capacity has grown sufficiently, it would be foolhardy to destroy our capacity for basic and applied work in our government institutions. Indeed, in the most highly developed countries, it is found that government and industry not only complement one another in research capacity, but that financial co-operation between government and industry is required to produce a progressive and productive climate (3). Certainly we should build our industrial research activity, but we should not be destroying the capacity for doing such work wherever it is done in our country today.

Funding of Research and Development

The general concensus which is developing is that although the total expenditure on research and development in the country is not excessive, (1.3% of the gross national product) (5), and indeed is proportionately less than that expended by several other countries with whom we are competing, the distinction of these funds is not consistent with that required to stimulate a high return on our scientific investment. Generally speaking, people feel that too much fundamental research is being done and not sufficient applied research and development (4). There will be a temptation to try and divert funds from the fundamental research activity into the more applied areas. Carried to an extreme, this could be an important mistake. Even in the U.S., the question of the level of support for basic science is so difficult a problem that funding levels are based more on empirical experience than on objective pragmatic grounds. However, as a datum from which to work, we cannot ignore the empirical experience of nations with a fully developed industrial structure. The magic number which has resulted from U.S. experience is of the order of 10% of total R and D (6). For two reasons which are peculiar to Canada, this number is not apt to be high enough:

a) Because we are a small nation, the proportion of funds that we spend to keep informed and alert to important developments in the rest of the world is inevitably going to be larger.

b) For the next decade, we will probably be producing scientists at a level consistent with a more fully developed industrial structure than will prevail. It is likely we will want to hold the surplus intended for industrial research as a battery of talent in the basic research activity.

In the face of conflicting priorities, I think we will all have to admit that basic research is reasonably supported today. What worries me most is that we will be tempted to reduce this level of support in order to build our capacity for innovation. I therefore feel that the preservation of our core of basic research capability in Canada will really depend on how

successful we are in taking the initiative to develop the applied research activity. The mismatch between the public and the basic scientist it really too great to foster a meaningful communication. At least over the next decade, I believe that the applied scientist and engineer will have to act as patrons for fundamental research and that it is in the interests of all of us to build a strong community of such patrons. At Whiteshell, our primary mandate is applied research and development. Nevertheless, we find that we do need a fundamental research activity to monitor the quality of our work and to give us a sufficient number of good consultants so that our lines of attack are less likely to be in conflict with Nature. However, I find in practice that when I am soliciting funds I really do so on the basis of our applied research and development. The applied people are the first to support the allocation of a share of the funds to our fundamental research activity.

In summary, this is the picture which I see.

1) At the level empirically known to be necessary for a progressive society, fundamental research requires predominantly public patronage.

2) Our society is not sufficiently advanced that the required level of support can be solicited on the basis of cultural arguments only. The taxpaying public is now demanding a test of pertinence.

3) Because the mismatch between public and the fundamental scientist is so great, the fundamental scientist is apt to require his applied colleagues to act as spokesmen and intermediate patrons between the fundamental scientist and the public.

4) The level of our fundamental scientific activity is today no more than that which is consistent with an advanced industrial nation. However, Canada is not yet fully industrially developed and requires the injection of applied research, development and innovation in order to profit more fully from basic scientific investment.

5) To preserve the now adequate core of fundamental scientific activity, the fundamental scientist can profitably take the initiative to test his program for pertinence. If alternative programs are being considered, it would be rewarding to lean towards those which can be supported on more utilitarian grounds. To a certain extent, the division between fundamental and applied work is a matter of outlook. To the extent that he himself has chosen the problem, the scientist is doing basic research. To the extent that the problems are of significance to industry and the public his work would be labelled applied. In a skillfully directed laboratory the amount of basic research can vary by a factor of as much as five, depending on whether one canvasses the scientists or their director.

Entomology in Context

Now then, how does the entomological community fare in comparison with this more general picture?

In the course of educating myself before this address, I have discovered that the study of insects has a long and distinguished history in Canada. The Entomological Society of Ontario, the parent of your present society, was founded in 1863 and was preceded by only two other scientific societies - the Nova Scotia Institute of Science and the Medical Society of Nova Scotia. I have learned that the Canadian Forest Insect Survey is acclaimed as one of the best in the world and that the Canada Department of Agriculture Entomology Research Institute has one of the largest groups of insect systematists in North America, and uses one of the greatest collections on the continent (7).

As to the current size and disposition of the entomological community, I find apparent conflicts in figures between the various submissions to the Senate Committee, and figures taken from the membership in your Society (8). However, for my purpose it is sufficient to note that there are probably between 400 and 500 professional entomologists in Canada

today, and that this number is only 0.25 to 0.31% of the total population of scientists and engineers.

Regarding the growth in research capacity, probably the best index is the graduate student enrolment in Canadian universities as reported by the National Research Council (9):

Year	Number of Graduate Students Enrolled in Entomology
1958-59	44
1959-60	49
1960-61	75
1961-62	83
1962-63	86
1963-64	91
1964-65	90
1965-66	91
1966-67	110
1967-68	135
1968-69	98

The most noteworthy feature of these figures is that over the past decade our capacity to produce entomological scientists has increased by a mere 100 to 125%, while over the same period our capacity to produce Ph.D's in the whole of science and engineering has grown by a staggering 480% (2).

In the face of these figures it would be difficult to accuse entomologists of empire building. On the contrary, one is driven to seek an explanation for such a low profile.

As I go through my catalogue of requirements for a stable scientific community, I find that you have grounds not only for stability, but for considerable expansion. I envy the director charged with the responsibility of defending his entomological program in today's environment. Your discipline has an impact that spans the entire spectrum from cultural to economic.

Let us consider first your capacity for cultural contribution. Unlike many other disciplines which require sophisticated and expensive equipment, your contributions to the culture of our society are open to the appreciation of everyone. Your writers are articulate to the point of lyricism. Your lay readers can understand most of what you have to say and have access to their own laboratories both inside and outside their homes. In numbers, distribution, variety, behaviour and importance of its subjects, entomology offers a unique outlet for the exercise of man's creative curiosity - certainly a far more varied and stimulating diet than ornithology can offer the bird-watchers. I find it a little surprising that there is not a nationwide "Insect Watching Society" with amateurs of all ages. Why too is there not a "bug of the month" award offered by this prestigious society to amateurs who have made notable contributions and observations?

If confronted by cost-benefit analysts you can claim major achievements in the past and the potential for future contributions of enormous value. You are a critical part of two of our major industries - agriculture and forest products. Where diseases are communicated through an insect vector, your contributions are necessary to preserve the nation's health. Where the quality of living is threatened by biting pests, your contributions are necessary to bring relief. All of these benefits can be quantified with sufficient rigor to satisfy the most hardened banker.

If these do not suffice, let us turn our attention to the politician. Canada is sufficiently affluent today to concern itself with the quality of its environment. Thus we now need more sophisticated solutions to the old problems of insect control. What is more, the resilience with which insect populations respond to any perturbation would suggest that a continuous effort will be required to control them.

Surely we can anticipate legislation in the near future which will stimulate the formation of "environmental control" organizations as an established requirement of most

major industries whose effluents and products could influence our ecology. In this respect the atomic energy industry has set a good example by taking the initiative to monitor itself. Any team concerning itself with environmental problems would inevitably have to include entomologists - where are they to come from?

One of the major impediments to the development of our north is the insect problem - how can this barrier be removed economically and without adverse effects on the delicate ecology? Your contributions are imperative to provide the answers.

If we are to pull our weight in helping the underdeveloped countries of the world, surely entomologists are required to recover the 50% of harvests that is regularly reaped by insects. If we are to contribute to these countries' health, surely entomologists are required to control the insect carriers. Do we have enough highly trained entomologists to make a real impact on problems of such importance?

In short, I find little difficulty in accepting the case for the modest expansion proposed in your special brief to the Senate Committee (10). The difficulty I have is judging whether you have asked for enough. I am driven to ask myself whether or not your arguments are sufficiently well developed and put with sufficient force to allow those responsible to arrive at a properly weighted judgment regarding our national priorities.

I close with one question only - in view of the enormous benefits which you have to offer our society, do you really believe that you are expending sufficient of your energy on growth? From my brief study of your discipline, I find you highly responsible but conservative to an extreme.

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RADIONUCLIDE DYNAMICS IN INSECT FOOD CHAINS*

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ABSTRACT

Knowledge of food chain dynamics is a prerequisite to understanding the fate of chemical compounds in ecosystems, since food chains are the primary biological mechanisms for the dispersal and concentration of radionuclide contaminants in the environment. The dynamics of material transport along insect food chains has received considerable attention in recent years, and mathematical models have been developed describing the variables affecting the behaviour of radionuclides in food chains. Knowledge of uptake, assimilation and metabolic turnover of radionuclides have led to predictable models of transient behaviour of materials along food chains, resultant trophic level concentrations and efficiencies of trophic level exchange.

INTRODUCTION

Text book descriptions of food chains often have depicted simplistic prey and predator relationships. Recently, with growing interest in environmental quality and concern over the movement of pollutants in the environment, food chains have been looked upon in a slightly different aspect. The food chain is increasingly recognized as the primary biotic mechanism for dispersion of contaminants within and between ecosystems. Far too often food chains have been envisioned as mechanisms operating solely to concentrate pollutants as they move from prey to predator. Less often are they objectively recognized as ecological processes, with the net effect of concentration or dilution of materials during their transport along the food chain being dependent upon a complex of biological variables.

Actually the food chain is an ecological process evolved through evolutionary time whereby an organism is interconnected trophically with other components of its ecosystem. It is a process through which the organism can satisfy its nutritional needs prerequisite for existence and reproduction. (For dietary deficient nutrients it may act as a filter or, for unnatural hydrocarbon residues soluble in adipose tissue, it may serve as a means of concentrating environmental pollutants.) The food chain process is a dynamic system — a continuing state of flux responding to changes, direct and indirect, in its trophic interactions with the total environment.

In this paper we attempt to summarize current research in the field of food chain dynamics — experimentation frequently incorporating radionuclide tracer methodology — to explore current theory and speculate upon future developments. Radiotracer principles are utilized to illustrate the basic dynamic aspects of the food chain — uptake, equilibration (steady-state), and turnover — and some simple mathematical models are presented to translate how these phenomena interact and operate temporally to influence the transport of materials along food chains.

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UPTAKE, TURNOVER AND EQUILIBRIUM

Whole-body concentrations of chemical compounds in animals are a resultant function of a combination of physiological and environmental variables. These variables affect the parameters of biological uptake and turnover of the chemical compounds, and the environmental concentration of the compounds. Variations in any one of these parameters may produce marked differences in whole-body concentrations in the animals, with subsequent differences in concentration becoming apparent in the entire trophic level.

Biological uptake of radionuclides by arthropods often has been described as a double exponential system composed of a fraction of the ingested material which passes through the gut (p_1) and a fraction which is assimilated into body tissues (p_2) (Reichle 1969). This model of radioisotope uptake is depicted mathematically as

$$Q_t = Q_e - p_1 Q_e e^{-\lambda_1 t} - p_2 Q_e e^{-\lambda_2 t} \qquad (1)$$

where Q_t = whole-body concentration of radioisotope at time t, Q_e = the equilibrium whole-body concentration of radioisotope, λ_1 = an estimate of the turnover rate associated with unassimilated radioisotope ($p_1 Q_e$) and λ_2 = an estimate of the turnover rate of assimilated radioisotope ($p_2 Q_e$).

Differences in turnover coefficients between various chemical compounds or different species can significantly affect the time required for reaching equilibrium. The curves shown in Figs. 1 and 2 were derived from equation 1 by varying the values of λ_1 in five equal intervals between 0.032 and 0.096 and λ_2 in five equal intervals between 0.006 and 0.018 for two different equilibrium levels (Q_e = 260 and 130 dpm/mg for Figs. 1 and 2, respectively). These two families of curves serve to illustrate how variations in the biological elimination coefficients for unassimilated and assimilated fractions affect the biological uptake of elemental materials. For a given equilibrium level (Q_e), various environmental stresses on biological elimination rates (e.g., temperature) tend to either increase or decrease the time period required to reach this equilibrium value. For example, in Fig. 1, only 300 hrs are required to reach Q_e when λ_1 = 0.096 and λ_2 = 0.018; whereas Q_e is not reached even after 500 hrs when λ_1 and λ_2 are decreased to 0.032 and 0.006, respectively — an effect which could be due to a reduction in environmental temperature. The effect remains constant, for a given stress, even as the value of Q_e changes (Fig. 2) due to either fluctuations in environmental concentration of the radioisotope in question (biologically indeterminant equilibrium) or due to some change in the physiological requirements of the animal for the element (biologically determinant equilibrium). As uptake proceeds toward equilibrium, the contribution of the unassimilated fraction ($p_1 Q_e e^{-\lambda_1 t}$ of equation 1) to total body burden becomes progressively less significant.

The turnover time of an element is the reciprocal of the biological elimination coefficient (Reichle 1967). This value ($1/\lambda$) represents the time required for complete turnover of 100% of the chemical pool in the organism. When approximately 100% of an element in a food source is assimilated, the value λ_2 represents the turnover rate for that element in a particular tissue. When appreciable amounts of an element are not assimilated, however, a weighted turnover rate can be calculated which takes into account the relative proportions of ingested element that are assimilated or passed directly through the gut (Reichle 1969, Van Hook 1971, O'Neil 1971). From the data of the uppermost curve in Fig. 1, a value of 0.025 was determined for the modified turnover rate. This yields a turnover time of 40 hrs in this particular instance, indicating that it requires ca. 40 hrs for an amount equal to 100% of this nutrient pool to be turned over.

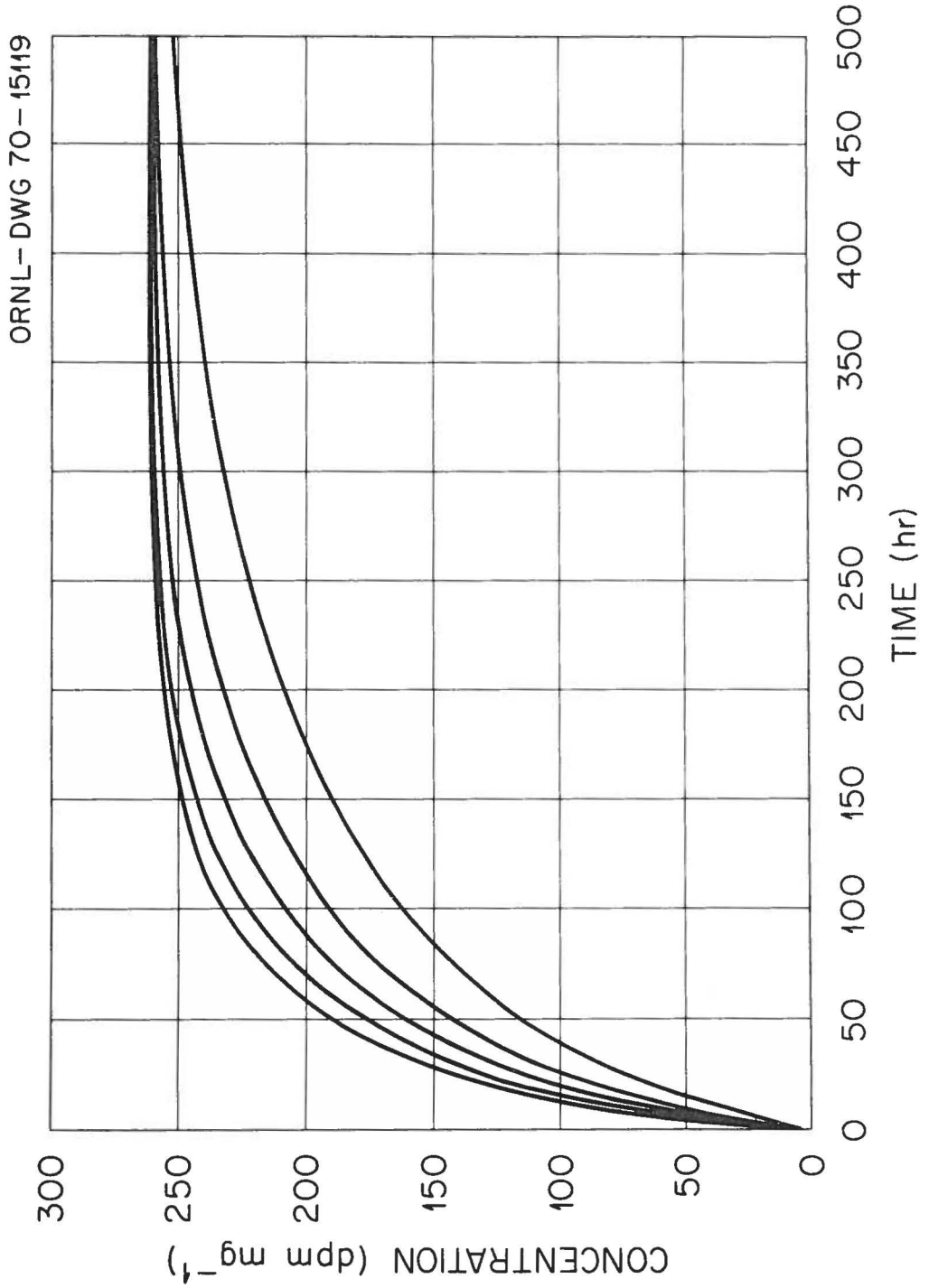

Figure 1. Radioisotope uptake patterns for an equilibrium whole-body radioactivity content (Q_e) of 260 dpm/mg derived from an assimilation value (p_2) of 0.66 with respective combinations of turnover rates λ_1 and λ_2 (.032, .006), (.048, .009), (.064, .012), (.080, .015) and (.096, .018).

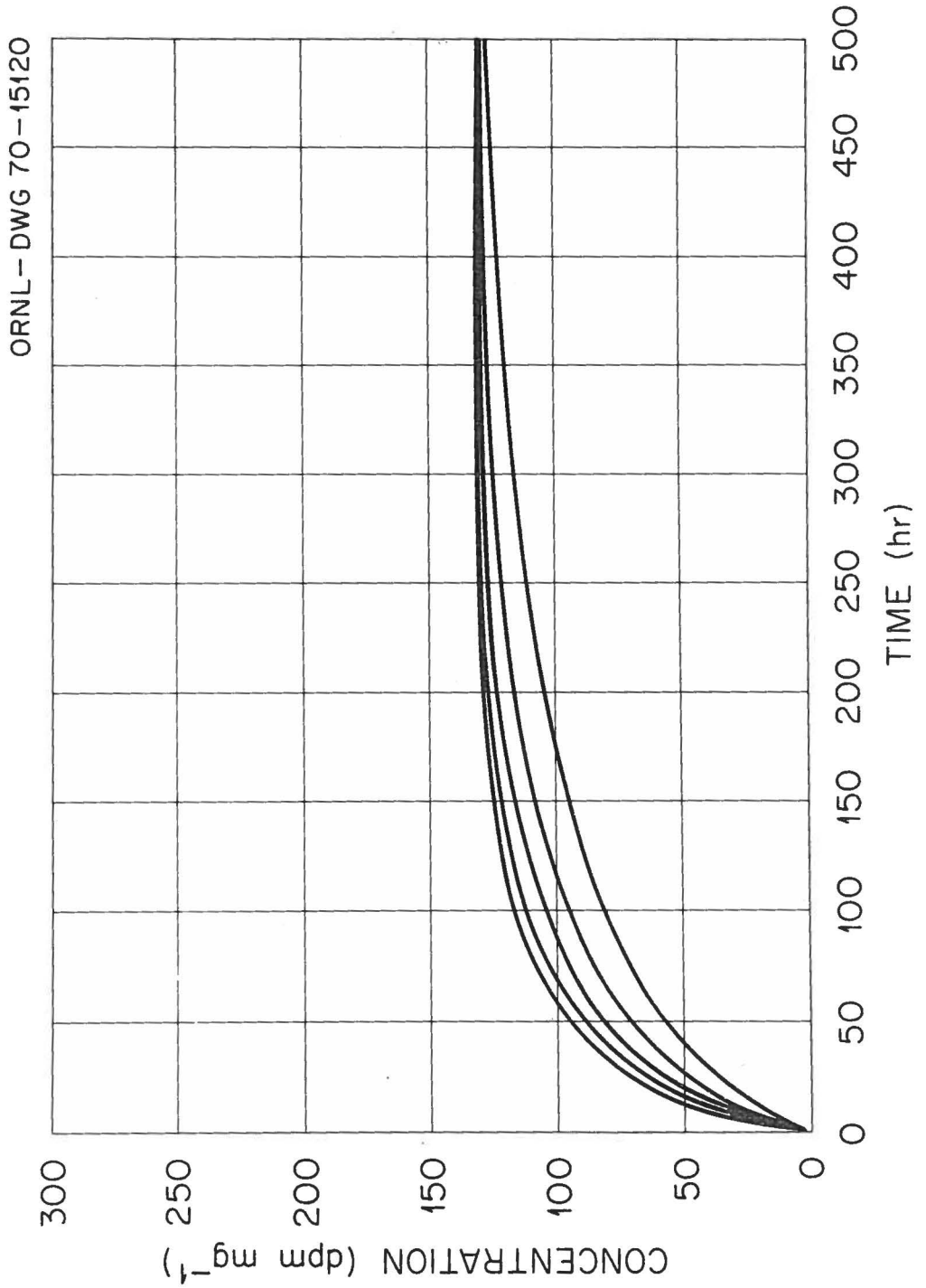

Figure 2. Radioisotope uptake patterns for an equilibrium whole-body radioactivity content (Q_e) of 130 dpm/mg derived from an assimilation value (p_2) of .066 with respective combinations of turnover rates λ_1 and λ_2 (.032, .006), (.048, .009), (.064, .012), (.080, .015) and (.096, .018).

STEADY STATE CONDITIONS – FACTORS AFFECTING CHEMICAL EQUILIBRIUM

Although various environmental and physiological variables affect the rates of uptake and turnover of materials, ultimate concentration factors for chemical compounds or elements are intimately related to the stable-element chemistry of the consumer organism and its food. Careful distinction should be made between elemental concentrations in organisms (ppm) and concentration factors for these elements in a food chain (ratio of ppm in organism to ppm in food).

Some organisms show relatively constant whole-body elemental compositions over a range of elemental concentrations in their environment. Under these circumstances, the elemental concentration factors are said to be *biologically determinant*, e.g., biologically constant and inversely proportional to increased concentrations of the respective elements in the environment. Many nutrient elements active in metabolic processes appear to be biologically determinant. Van Hook (1971) found no significant seasonal differences in the sodium, potassium and calcium content of grassland arthropods, although these elements varied through time in the grass food base. Similar relationships, although not without exceptions, have been reported for Na, K and Ca in forest arthropods' food chains (Reichle and Crossley 1967; Reichle *et al.* 1969). Organisms in food chains may concentrate these elements above levels in their food base, but once optimum whole-body concentrations are attained they remain constant despite subsequent fluctuation levels in their food.

Conversely, other classes of chemical compounds and elements have whole-body concentrations directly proportional to environmental concentrations. Elements which behave in this manner are *biologically indeterminant*. Such elements are often those which are not metabolically active, and uptake and excretion by the animal follow simple mass balance equilibria. Other such compounds are those for which the organism does not possess the capability for biological degradation and excretion, with resulting accumulation in certain body tissues. Although some environmental pollutants such as DDT and toxic heavy metals may be metabolized and excreted by the organism, their concentration appears biologically indeterminant. Additions of tracer quantities of biologically hazardous elements into the environment seldom have a significant effect on the total chemistry of those elements. Concentration factors for the tracer simply reflect availability, although whole-body concentrations may indeed be biologically determinant. The behaviour of ^{137}Cs in arthropods' food chains (Fig. 3) illustrates this point. Whole-body concentrations of ^{137}Cs are directly proportional to levels of radionuclide in food, even though total cesium concentrations in various diet items were essentially constant. These data were derived from foliage-feeding insects, although similar relationships can be shown for detritus-feeders and predators.

For radionuclide contaminants, the specific activity concept (Nelson 1966; Kaye and Nelson 1968) is one technique which permits *a priori* prediction of the steady-state distribution along food chains. Specific activity is defined as the ratio of radioactive atoms to total atoms of the same element. By using the stable element distribution in environmental samples, the dispersion of long-lived radionuclides can be calculated if the following are known: (1) the stable element chemistry of the organisms comprising the food chain and (2) the specific-activity ratio of the element at the source of its access to the food chain. Thus

$$\frac{\text{Radionuclide in food}}{\text{Total element in food}} = \frac{\text{radionuclide in consumer}}{\text{total element in consumer}}$$

This application is valid only if there is complete environmental mixing and no biological discrimination between the radionuclide and its stable-isotope analog. Although steady-state conditions may be estimated quite accurately from specific activity ratios and stable-element chemistry, this approach does not provide insight into the dynamics of the system, e.g., the rates of exchange between trophic levels of the food chain and the time required for equilibration at each level.

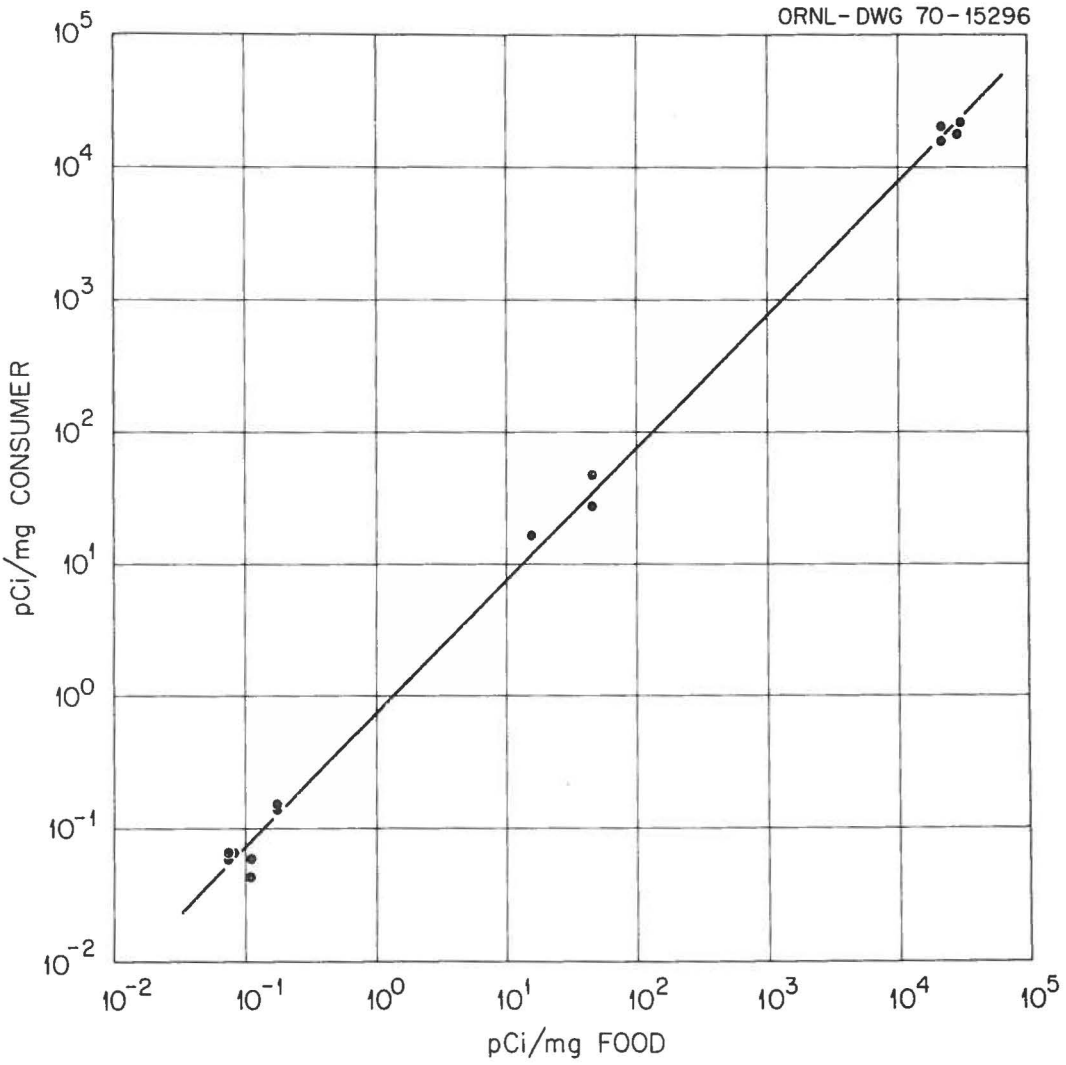

Figure 3. Linear relationship between concentration of ^{137}Cs in food and resultant equilibrium body burdens in foliage-feeding insects, $\lambda = 0.74X^{1.01}$. Thus, radiocesium concentrations in insects appear to be biologically indeterminant, e.g., directly proportional to environmental concentrations. Data after Crossley and Howden (1961), Reichle (1967) and Reichle and Crossley (1967).

FOOD CHAIN DYNAMICS

A food chain is a dynamic process characterized by the continual exchange and redistribution of materials among its component parts. These food chain transfers are not instantaneous; characteristically, temporal delays exist in the flux of materials between trophic levels. This results in time lags for successive trophic levels to attain maximum concentrations, following introduction of the material into the food chain. Where the distribution of radionuclides along food chains has been examined, the application of intake-loss mass balance equations can provide valuable estimates of fluxes between successive links in the food chain (Crossley and Reichle 1969).

For animals feeding upon a contaminated food source (such as one tagged with ^{137}Cs), the change in radionuclide concentration with time is given by the intake-loss balance equation

$$\frac{dQ}{dt} = IA_o e^{-\lambda_a t} - \lambda_q Q \qquad (5)$$

where Q is the radionuclide concentration in the consumer animal, I is the intake rate of food (i.e., mg food per mg consumer per day), A_o is the initial concentration of radionuclide in the food base, λ_a is the turnover coefficient of radionuclide from the food, and λ_q is the turnover coefficient for the radionuclide in the consumer organism. Turnover coefficients are equal to $0.693/T_{1/2}$, where $T_{1/2}$ is the half-time or biological half-life. For short-lived radionuclides where physical decay is an important parameter, biological (λ_b) and physical (λ_p) loss coefficients are additive, i.e., $e^{-(\lambda_b+\lambda_p)t}$. Radionuclide concentration in the consumer organism as a function of time is the solution to the differential equation

(5) $$Q(t) = \frac{IA_o}{\lambda_q - \lambda_a}\left[e^{-\lambda_a t} - e^{-\lambda_q t}\right] + Q_o e^{-\lambda_q t} \qquad (6)$$

where Q_o is the initial concentration of isotope in the consumer. If no previous body burden of radionuclide was present in the consumer, $Q_o = O$ and $Q_o e^{-\lambda_q t}$ may be dropped from equation (6). The time required for maximum concentration to occur in the consumer is obtained by setting the derivative of equation (6) equal to zero and algebraically solving for t_{max}

$$t_{max} = \frac{1}{\lambda_q - \lambda_a} \ln \frac{\lambda_q}{\lambda_a}, \qquad Q_o = O \qquad (7)$$

Since successive trophic levels in a food chain show delays in exchange of chemical compounds, the temporal behaviour of radionuclide tags introduced into food chains can be used to delineate trophic position of the organisms involved. Figure 4 illustrates the temporal changes in ^{137}Cs concentrations in a detritus-fungus-saprophage-predator food chain of a forest ecosystem (McBrayer and Reichle 1971). Litter tagged with ^{137}Cs (11.1 x 10^3 dpm/mg) added to soil microcosms resulted in an immediate bloom of fungi (4.77 x 10^3 dpm/mg). Soil animals feeding upon these food bases showed the characteristic uptake curves in Fig. 4. Fungivores exhibited rapid uptake of ^{137}Cs, but then decreased to lower equilibrium values as the fungal bloom was exhausted. Saprovores, feeding upon a mixture of detritus and fungus, also exhibited immediate ^{137}Cs uptake and equilibrated at a value approximately equal to that of their food. Predators showed delayed radionuclide uptake and equilibrated at only 0.3 the concentration of their prey.

Crossley and Reichle (1969) monitored the transient behaviour of ^{137}Cs in forest insect food chains and were also able to resolve the time differential for average radionuclide transfer times between successive trophic levels: 60 days from plant to consumer and 30 days from primary consumer to predator. These data demonstrate that, although the

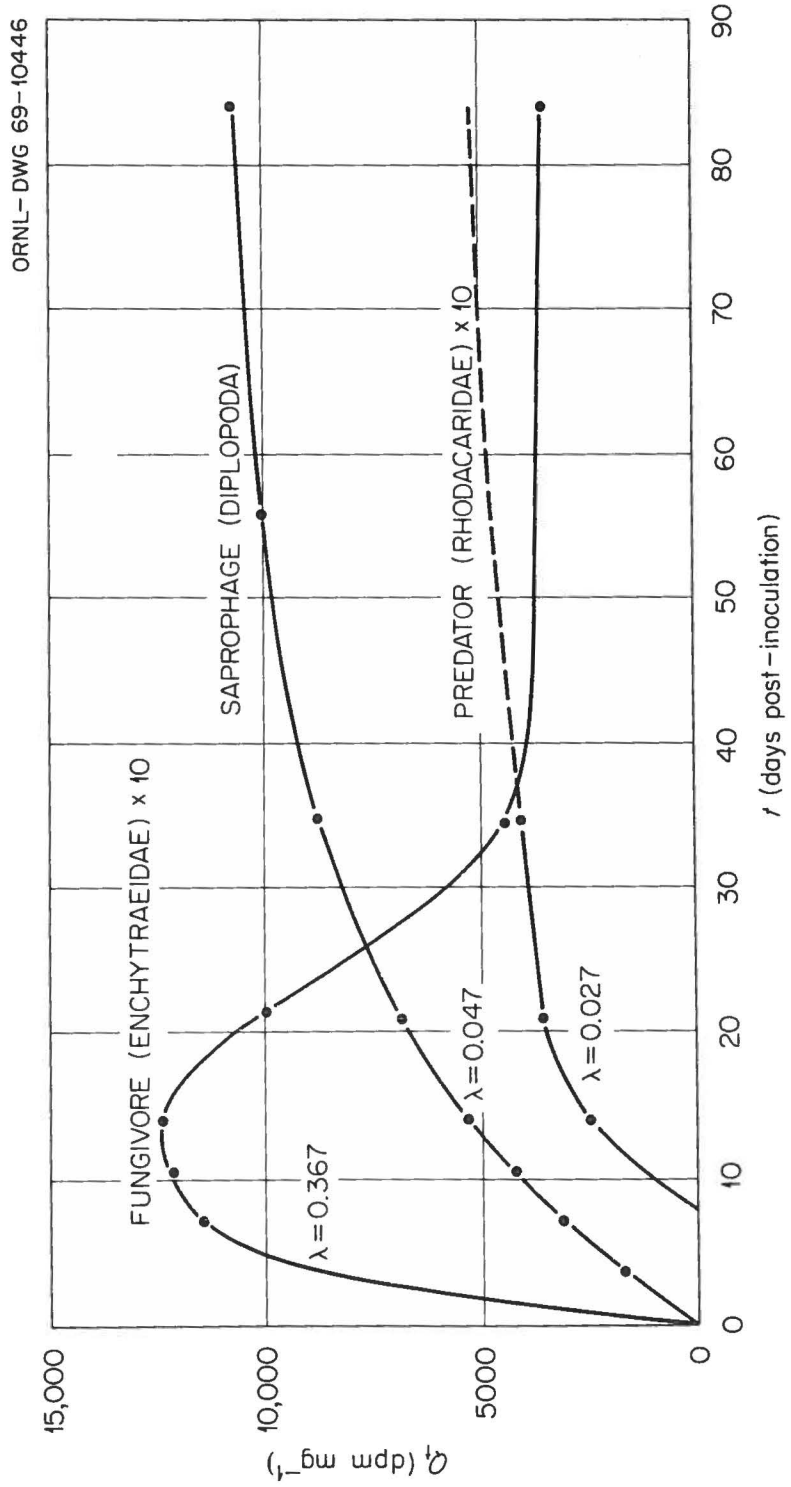

Figure 4. Transient behaviour in whole-body concentrations of ^{137}Cs (Q_t) in successive trophic levels of a detritus-based food chain. Radionuclide tag was introduced into litter; λ 's represent uptake rates (proportion of equilibrium concentration accumulated per day) by respective consumer organisms. Data after McBrayer and Reichle (1971).

absolute amount of radionuclide may decrease in passage up the food chain, the relative mobility and turnover time of the material is accelerated. Whether this is a fundamental attribute of food chains has yet to be unequivocally demonstrated.

Trophic level concentration factors for nutrient and non-nutrient elements differ because of differences in the absolute concentration in initial links of food chains. Data from Table 1 serve to illustrate this for a forest floor food chain; while some essential nutrients are concentrated in their movement up the food chain (K, Na, P and N), others are diluted (Ca). Food chain concentrations reflect the physiological requirements of arthropods for these elements and the availability of these elements from the environment — those required in substantial quantities for metabolic processes and in scarce supply tend to be concentrated by the food chain, while non-essential elements may or may not be accumulated. Although the data of Table 1 are similar for calcium and sodium when compared with food chain concentration factors for an arthropod community in a grassland ecosystem (Van Hook 1971), potassium was diluted in its movement through the grassland arthropod food chain. The lower concentration factor in the herbaceous food chain was due primarily to higher potassium levels in the grass food base. Calcium was not accumulated by either the detritus or the herbaceous food chains.

Food chains transfer efficiencies can be utilized in describing nutrient transfer between successive trophic levels and nutrient redistribution within recipient trophic levels. Trophic level transfer ratios (ingestion at trophic level n/ingestion at trophic level n-1) and progressive assimilation efficiencies (assimilation at trophic level n/assimilation at trophic level n-1) reflect the efficiency of movement through the food chain. The values for these ratios for nutrients generally range from 10 to 20% of their respective energy values, indicating that nutrient mobility along food chains is less efficient than that of energy (Van Hook 1971). Consumption efficiencies depicting the transfer of nutrient elements between successive trophic levels (ingestion at trophic level n/net production at trophic level n-1) vary considerably among elements and trophic levels. For example, values for consumption efficiencies for herbivores in a grassland community range from 2 to 11% for potassium and calcium, respectively, with the value for sodium being intermediate (8%) (Van Hook 1971). Consumption efficiencies for these three nutrients in grassland predators are somewhat more consistent, ranging only from 2 to 5%. Assimilation efficiencies (assimilation/ingestion), reflecting the fraction of ingested nutrient incorporated into the biomass and utilized by the trophic level, are similar for sodium and potassium in the grassland food chain; 90, 75 and 60% for herbivores, omnivores and predators, respectively. Assimilation efficiencies for calcium were different from those of sodium and potassium for each of the three trophic levels studied. From these data, it appears that the efficiency of net nutrient transfer decreases with increasing trophic position in arthropod food chains.

CONCLUSIONS

Through study of the variables affecting the dynamic food chain process we have begun to understand the factors affecting the food-chain dynamics of materials and, ultimately, their long-term fate in the biota. Potential movement of materials throughout the biota of natural ecosystems involves enumerable variables such as dietary levels in food, physiological state of the consumer, ingestion rates, whole-body chemistry, biological degradation and turnover (excretion) rates. Often cause and effect between these parameters is such that specific values are applicable only in the situation of the particular food chain being examined.

Therefore, it is fallacious to attempt to categorize the food chain as either a concentrator or filterer of constituents in the environment — whether nutrients or pollutants. Behaviour of these materials is but only the product of the food chain process and, *a priori* generalizations without adequate understanding of the process, may lead to erroneous assumptions. These examples caution for judiciousness in developing broadly-based assumptions on food-chain behaviour from data obtained from unrelated studies; yet by illustrating basic principles of the food chain which differ in degree and not kind, they offer encouragement for more studious interpretations of this basic ecological process.

TABLE I

Concentration factors of several important nutrient elements from plant leaves through 3 invertebrate trophic levels in a forest floor community. Concentration factors were derived from element contents (mg element per g dry wt) by setting plant values at unity. Data after Reichle, Shanks and Crossley, 1969; nitrogen value estimated from Satchell, 1967.

Trophic Level	Ca	K	Na	P	N
Plant Leaves	1.0	1.0	1.0	1.0	1.0
Saprovore	0.1	3.5	17.0	11.0	10.0
Herbivore	0.1	3.0	21.0	17.0	—
Predator	0.1	2.0	27.0	18.0	—

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RADIOECOLOGY OF INSECTS IN AQUATIC ENVIRONMENTS

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ABSTRACT

Radioecology is the study of the relationship of radioactive substances and ionizing radiation with the environment. One aspect of this study pertinent to entomology is the uptake and distribution of radionuclides by insects. The accumulation of radio-isotopes by aquatic insects is reviewed with emphasis on the uptake of radiocesium, a biologically important nuclear fission product, by insects living in an experimental pond contaminated with ^{137}Cs. The relationship between the distribution of the nuclide in the pond and the levels of radioactivity accumulated by Chironomid larvae and free-swimming (nektonic) insects, is examined. A pyramid of specific activities (dpm/g wet wt.) is shown to be a useful method for summarizing the results, and it suggests the primary food sources of the major insect species living in the pond.

Radiotracer techniques have been used by several workers studying the feeding and assimilation rates of terrestrial phytophagous insects. The uptake and elimination of ^{137}Cs by *Lethocerus americanus* and *Aedes aegypti* larvae has been investigated in the laboratory, to assess the feasibility of using this nuclide to measure food consumption in aquatic habitats.

INTRODUCTION

One aspect of radioecology pertinent to entomology is the accumulation of radionuclides by insects living in aquatic habitats. The increasing number of nuclear power stations and the associated release of low-level radioactive wastes into the environment, necessitates studies of accumulation and elimination of radioactive isotopes by various components of biotic communities (Wilhm, 1970).

Aquatic insects, a significant component of aquatic communities, may become radioactive by adsorption of radionuclides on exposed surfaces, absorption into tissues from the water, or as a result of ingesting food contaminated with radioactivity (Davis and Foster, 1958). The movement of radionuclides through food chains is of interest to ecologists for several reasons. The food consumption and assimilation of organisms may be estimated by labeling the food source with a radioactive tracer, or population dispersion may be measured by tagging insects with a suitable isotope (O'Brien and Wolfe, 1964). The question of to what extent radionuclides are concentrated by aquatic insects is of more than academic interest. Russian workers have suggested that the radioactive contamination of aquatic organisms is close to a level which threatens their biological activities (Polikarpov, *et al.*, 1966). It has also been suggested by Peredel'skii and Bogatyrev (1959) that insects emerging from radioactive ponds may contaminate the surrounding terrain. The work of other investigators and our experience at Whiteshell does not support this view. However, Krumholtz (1954) was able to detect above-background levels of radioactivity in insects emerging from White Oak Lake which at one time received the low-level radioactive liquid wastes discharged from the Oak Ridge National Laboratory. Because many radionuclides are

present in aquatic ecosystems, the ecologist is also provided with a unique tool with which to study trophic level kinetics, food-web relationships, and productivity (Schultz and Klement, 1963; Odum, 1959; Olson, 1965; and Reichle, 1967). I propose this morning to briefly discuss some aspects of radionuclide uptake, particularly ^{137}Cs a biologically important fission product, by aquatic insects. As it is a gamma emitter that is predominantly distributed throughout the haemolymph and muscle of terrestrial insects (Cavalloro, 1966), repeated measurements of ^{137}Cs can be made on the same individual by gamma spectrometry.

Radionuclide Uptake by Aquatic Insects

Excluding radiation effects, entomological work utilizing radioisotopes has focused on 'tagging' procedures for studying population dispersion, investigation of metabolic pathways (O'Brien and Wolfe, 1964), and more recently turn-over and food consumption studies (Crossley and Howden, 1961; Crossley, 1966, for example). Fewer investigations have been made of aquatic species than of terrestrial species.

The **concentration factor** is a convenient index with which to express an organism's ability to concentrate constituents in its environment. According to Harrison (1967), a true concentration factor can be approximated by determining the ratio of the radionuclide concentration in a representative population in equilibrium with its biological exchangeable pool. Harrison stresses that before concentration factors are used for the assessment of radioactive contamination of food-chains, the method of measurement should be examined to ascertain if it is applicable to the situation under study. Chapman *et al.* (1968) have compiled a list of radionuclide concentration factors for edible plants, invertebrates and fish.

To date, the most extensive reports on radionuclide uptake and concentration by aquatic invertebrates are those of Krumholtz (1954), Krumholtz and Foster (1957), Davis (1962), and Polikarpov (1966). More than 25 radionuclides have been found in some 30 genera of aquatic insects. A list would include:

^{24}Na, ^{32}P, ^{35}S, ^{46}Sc, ^{51}Cr, ^{54}Mn, ^{59}Fe, ^{60}Co, ^{64}Cu, ^{65}Zn, ^{76}As, ^{86}Rb, $^{89,90}Sr$, ^{91}Y, ^{95}Zr-^{95}Nb, $^{103,106}Ru$, $^{134,137}Cs$, ^{140}La, $^{141,144}Ce$, ^{203}Hg, and ^{239}Np.

Krumholtz (1954), studying the limnology of White Oak Lake, has measured total radioactivity in Odonata, Hemiptera, Plecoptera, Coleoptera, and Diptera including black-flies. He estimated the radioactivity of the *Tendipes* to consist of 50% ^{32}P, 6.6% $^{89,90}Sr$, 3.3% ^{137}Cs, and 6.0% total rare earths. Cesium-137 in particular, has been reported to be accumulated by Odonata nymphs (Pendleton, 1962; Volkova, 1963), Caddis-fly larvae (Volkova, 1963), Belostomatidae nymphs and adults (Guthrie and Brust, 1969), Chironomids (Wilhm, 1970), mosquitoe larvae (Getsova and Volkova, 1962; Guthrie and Burzynski - unpublished data), and Ephemeroptera nymphs (Volkova, 1963).

Radiation as an Ecological Stress

To illustrate the use of ^{137}Cs in aquatic insect studies, I shall describe two investigations currently in progress at WNRE. The first describes a study to investigate the feasibility of using radiation as an environmental stress. In November 1965, two ponds were dug in the edge of a stand of young poplars *(Populus tremuloides* and *P. balsamifera),* adjoining an old field. The ponds were lined with 5 mil black plastic sheeting to reduce water loss, and the sheeting covered with a 15 cm thick layer of the excavated soil. The ponds measured 19 m in diameter and sloped uniformly down to the center to a maximum depth of 2 m. After the spring thaw of 1966, both ponds were full of water as a result of melting snow and spring rainfall. No plant or animal life was artificially introduced into

either pond. The pond communities developed by invasion from the surrounding terrain, or by chance introduction of renewal buds or other reproductive bodies with the excavated earth used to cover the plastic sheeting. In May 1967, 0.5 Ci of carrier-free ^{137}CsCl solution was mixed with the water of one of the ponds, subsequently called the Active Pond. The level of ^{137}Cs in the other pond, designated the Non-active Pond, was about 0.001 dpm/ml, and is attributed to fallout.

After adding ^{137}Cs to the Active Pond, the water was sampled to determine the rate at which the radiocesium concentration in the water decreased. These measurements are summarized in Fig. 1, where the ^{137}Cs activity of the water in disintegrations per minute per ml (dpm/ml) is plotted against time. It will be seen from this figure that the initial rapid decrease in ^{137}Cs concentration levelled-off at 3 dpm/ml by May 1968. The level measured in the Non-Active Pond at this time was still about 0.001 dpm/ml. The major decrease occurred during the 20 day period that followed the addition of ^{137}Cs to the Active Pond (Fig. 1) and is attributed to sorption by the pond sediment (Guthrie and Scott, 1969). The disappearance of ^{137}Cs from the water then continued at a slower rate before levelling-off 75 days later. The latter decrease is attributed to radiocesium uptake by the pond biota (Davis, 1963; Seymour, 1964). Compared with the center of the Active Pond, a relatively large radiation dose was delivered to benthic organisms living in the vicinity of the pond margin, where in some locations the total dose delivered during May - October 1967 exceeded 200 Rad (Guthrie and Scott, 1969).

Chironomid larvae (*Glyptotendipes* sp., *Polypedilum* sp., *Psectrotanypus* sp., and *Acriotopus* sp.) inhabited both ponds. These populations have been sampled each summer since 1966, with ten or more random samples being taken at one time from each pond. The means of each set of samples are given in Fig. 2 where it will be seen that the maximum number of chironomids taken from the Non-active Pond each year lagged behind that of the Active Pond in 1968 and in 1969. A rank sum test (Wilcoxon and Wilcox, 1964) was used to test the difference and variability of the means (unpaired replicates), and the results are summarized in Table I. The tests reported in this table indicate that the variability of the samples taken at the same time was the same for both ponds. However, one year after the Active Pond was contaminated significant differences between the pond means ($p = 0.01$) began to appear. Two known dissimilarities between the ponds that might account for this observation are: 1) the bottom temperature of the Non-active Pond was 2°C colder than that of the Active Pond during May to August, 1968, and 2) Chironomids living in the Active Pond received an annual radiation dose of at least 50 Rad, and as much as 500 Rad depending on their location in this pond. Nelson (1967) has reported chromosomal aberrations occurring in *Chironomus tentans* which he attributed to radiation. He pointed out, however, that the induced aberrations were eliminated from the population by natural selection, hence no permanent radiation damage to the population was demonstrated. We have also observed that a greater number of species of algae invaded the Non-active Pond, and that blue-green algal growths were dominant in the Active Pond (Dugle and Guthrie, 1970). Tardigrada are present in the Non-active Pond but since 1968, none have been taken from the Active Pond. As this work was only a feasibility study, we plan to build more ponds of the type described to investigate these differences more thoroughly.

Uptake of ^{137}Cs by Insects

Environmental radiation studies have demonstrated the tendency of some radionuclides to accumulate rapidly in the primary producer trophic-level, and certain nuclides may be apparently concentrated in the higher trophic levels (Schultz and Klement, 1963; Åberg and Hungate, 1966). Pendleton and co-workers have suggested that radiocesium is concentrated at each successive level of the food-chain, as it passes from primary producers to primary and secondary consumers (Pendleton, 1962; Pendleton and

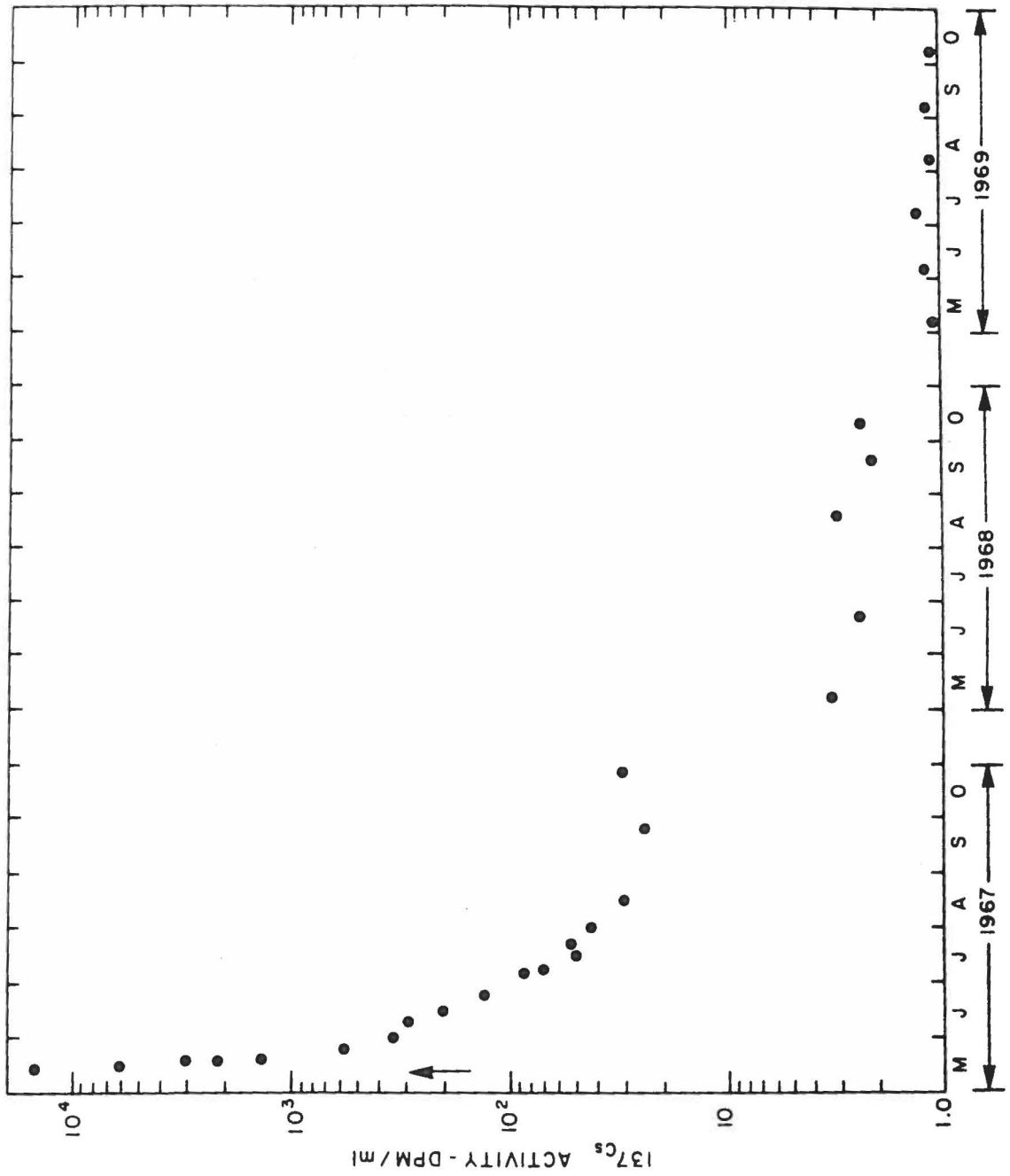

Figure 1. ^{137}Cs concentration in the water of the Active pond after addition (↑) of radionuclide on 11 May 1967.

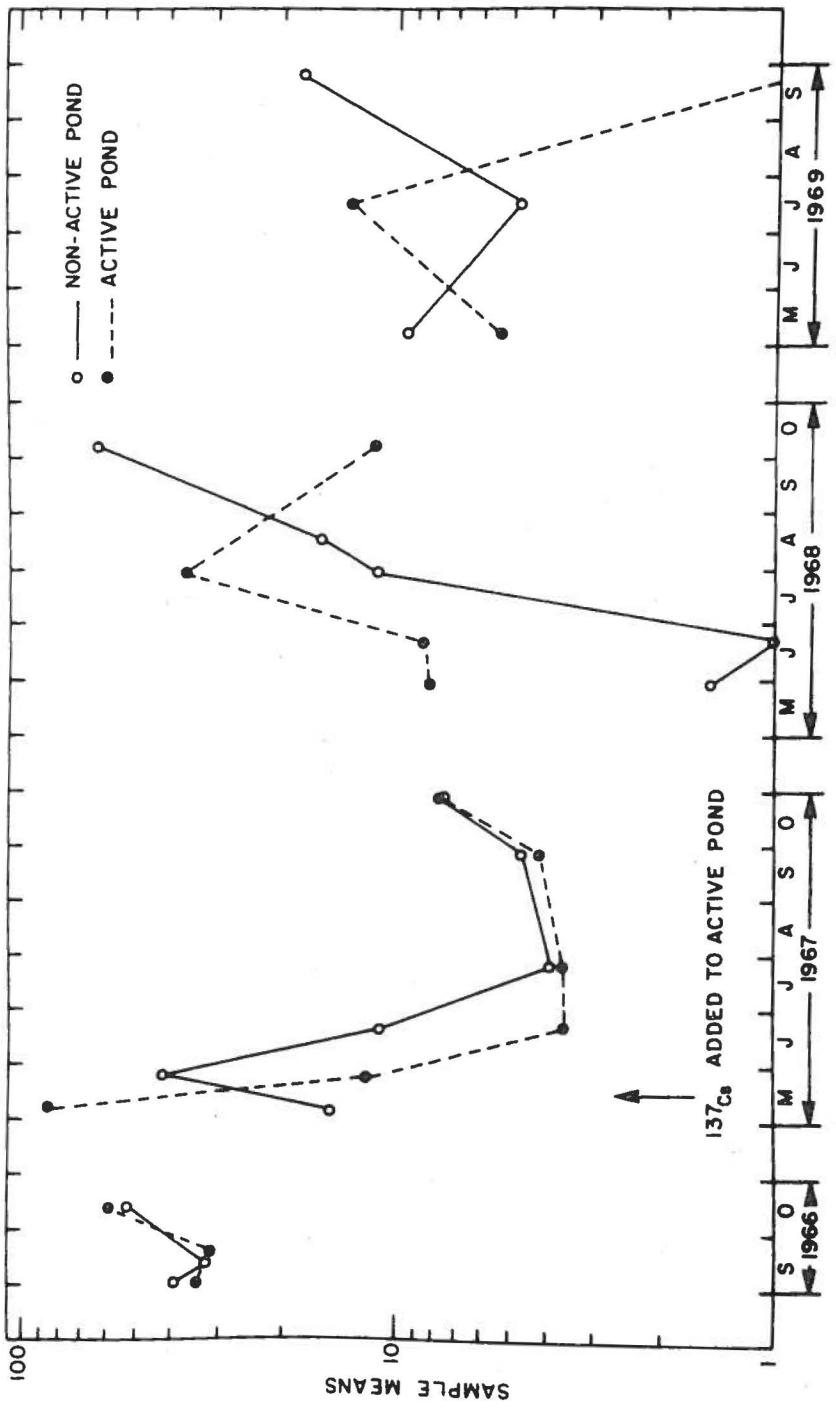

Figure 2. Mean number of chironomid larvae sampled at various times from the Active and Non-active ponds.

TABLE I

Mean number of Chironomid spp. larvae sampled from Non-active and Active ponds 1966-1969

ND = no difference. See text for details of sampling procedure.

Month	Non-Active Pond (NA) Mean of samples	Active Pond (A) Mean of samples	Test of Differences (1) p = 0.01 Means	Variability
1966				
1 Sept.	38.9, N = 23	34.0, N = 22	ND	ND
12 Sept.	32.4, N = 19	30.6, N = 20	ND	ND
13 Oct.	52.7, N = 19	59.0, N = 20	ND	ND
1967				
8 May	15.2, N = 10	84.6, N = 10	ND	ND
^{137}Cs added to Active Pond				
24 May	42.4, N = 10	12.0, N = 10	ND	ND
20 June	11.4, N = 10	3.6, N = 9	ND	ND
25 July	3.9, N = 10	3.6, N = 10	ND	ND
26 Sept.	4.7, N = 10	4.2, N = 10	ND	ND
24 Oct.	7.5, N = 10	7.7, N = 10	ND	ND
1968				
28 May	1.5, N = 10	8.2, N = 10	NA < A	ND
21 June	0.7, N = 10	8.6, N = 10	NA < A	ND
29 July	11.4, N = 10	36.1, N = 10	NA < A	ND
19 Aug.	16.2, N = 10	25.8, N = 10	ND	ND
7 Oct.	60.3, N = 10	11.5, N = 10	ND	ND
1969				
6 May	9.7, N = 10	5.4, N = 10	ND	ND
15 July	4.8, N = 10	13.5, N = 10	NA < A	ND
24 Sept.	18.2, N = 10	0, N = 10	A < NA	—

(1) Wilcoxon and Wilcox (1964) Rank Sum Test for testing the difference in means and variability in unpaired replicates.

Hanson, 1958). This suggestion has been challenged by other investigators. The work of Nelson and his colleagues (Nelson *et al.*, 1967) indicates that trophic-level increases may not be the general rule in aquatic environments since the observed differences appear to be the result of different food-chains in different habitats. These workers concluded that available data did not warrant application of trophic-level increases to cesium in aquatic food-chains.

The concentration of ^{137}Cs in some insect species living in the Active Pond has been followed since 1967. The ^{137}Cs activities are summarized in the histogram (Fig. 3) where the measurements are reported as the weighted mean activity of all the samples of each family (Table II) sampled during the months of April to October, in 1967 through 1969. The Active Pond was not sampled as frequently in 1969, as in preceding years, which may account for the absence of some of the species that year. It can be stated however, that the giant water bug *(Lethocerus americanus)* was abundant in the Active Pond in 1967, but absent in 1968 and 1969. To date, Ephemeroptera nymphs and Chironomid larvae have accumulated the greatest amounts of ^{137}Cs, and the activity of these species has decreased each year (Fig. 3). The radiocesium activities of the other families were about one order of magnitude less than those of the Ephemeroptera and Chironomids. It should also be noted that the levels of ^{137}Cs accumulated by Hemipterans and Coleopterans did not decrease nearly as much between 1967 and 1968, as did the Ephemeroptera and Chironomids, in contrast to the period 1968-1969.

The apparent grouping of insect ^{137}Cs activities given in Fig. 3 suggested that it might be informative to arrange the families according to their feeding habits, thus relating ^{137}Cs activity to trophic-level. In Fig. 4, the insect families have been assigned to trophic-levels according to feeding habits. The radiocesium activities of the Active Pond bottom ooze, algae and tadpoles (unpublished data) are also shown in this figure. Trophic-level appears on the left-side of Fig. 4. The grand mean ^{137}Cs activity of each level was calculated by summing the activities of each family (Fig. 3) assigned to that level, and it is shown on the right-side of Fig. 4.

Fig. 3 is based on insect activity, and Fig. 4 according to trophic-level. The stratification of insect families apparent in the latter figure constitutes a pyramid of radioactivity. Fig. 4 suggests that insect families within the same order of magnitude of ^{137}Cs activity were primarily feeding from the same trophic-level of the Active Pond food-web. Although the use of insect radioactivity alone may not enable one to assign an insect to the correct level, it appears that radiocesium, used as an ecological tracer, offers a useful field method for assigning aquatic insects to their appropriate trophic-level.

The distribution of ^{137}Cs through the chain depicted in Fig. 4 can also be described in terms of concentration factors, that is the radioactivity of a given trophic-level divided by the activity of the preceeding level (Pendleton, 1962; Harrison, 1967). The concentration factor (CF) calculated from the data given in Fig. 4 appears on the right-side of this figure under ^{137}Cs activity. In the Active Pond, radiocesium was concentrated by a factor of 0.1 at the primary consumer level. Between this level and that of insect predators (primary and secondary consumers), the concentration factor decreased to 0.01. Clearly then, ^{137}Cs was not concentrated at successive trophic-levels by the Active Pond insects which were studied.

Physiological Applications of Radionuclides

I would like to conclude this paper with a brief reference to a somewhat more physiological application of ^{137}Cs to entomological studies. The technique of food consumption and assimilation estimation using radionuclides has been applied by several workers, (Crossley and Pryor, 1960; Crossley and Howden, 1961; Kevern, 1966; and Reichle, 1967) and Dr. Reichle in his paper has discussed the application to trophic-level efficiency estimation. To my knowledge ^{137}Cs has only recently been used to measure food consumption by an aquatic insect (Guthrie and Brust, 1969).

TABLE II

Aquatic insects sampled from the Active pond in 1967, 1968 and 1969 for ^{137}Cs counting.

? indicates a tentative identification

Order	Family	Genus	Species
Coleoptera			
	Dytiscidae (predacious diving beetles)	Acilius	*A. semisculcatus* (Aubé)
		Colymbetes	*C. scultptilis* (Harris)
		Dytiscus	*D. cordieri* Aubé
			D. fasciventris Say
			D. dauricus Gebl.
		Ilybius	*I. fraterculus* Lec.
		Rhantus	*R. frontalis* Marsh
	Gyrinidae (whirligigs)	Gyrinus sp.	
Diptera			
	Chironomidae (non-biting midges)	Glytotendipes	
		Polypedilum	
		Psectrotanypus	
		Acricotopus	
Ephemeroptera			
	Baetidae		
		Baetis	
		Caenis	*C. ? simulians*
Hemiptera			
	Belostomatidae (giant water bugs)	Lethocerus	*L. americanus* (Leidy)
	Gerridae (water striders)	Gerris	*G. dissortis* Drake and Harris
		? Metrobates	*G. ? remigis* Say
	Notonectidae (backswimmers)	Notonecta	*N. undulata* Say
			N. borealis Bueno and Hussey
Odonata			
	Libellulidae	Libellula L.	
	Gomphidae	Opeogomphus	
			O. ? colubrinus (Say)

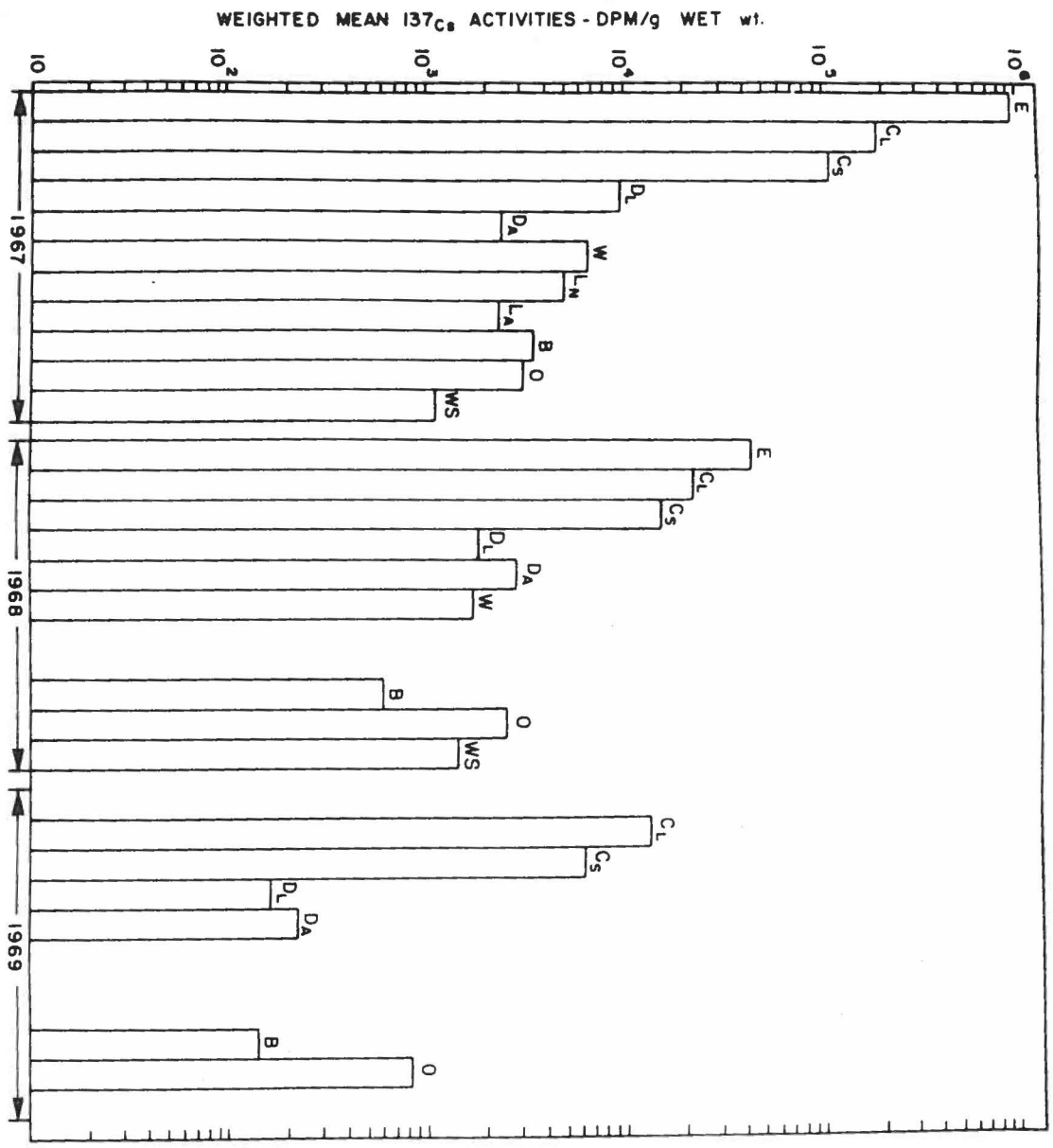

Figure 3. Weighted mean ^{137}Cs activities of insects (see Table II) collected from the Active pond.

E - ephemeroptera nymphs
C_S - chironomid larvae, early instar
D_A - dytisic adults
L_N - giant water bug, 4th instar
B - backswimmer adults
WS - waterstrider adults
C_L - chironomid larvae, late instar
D_L - dytiscid larvae
W - whirligig adults
L_A - giant water bug adults
O - odonata adults

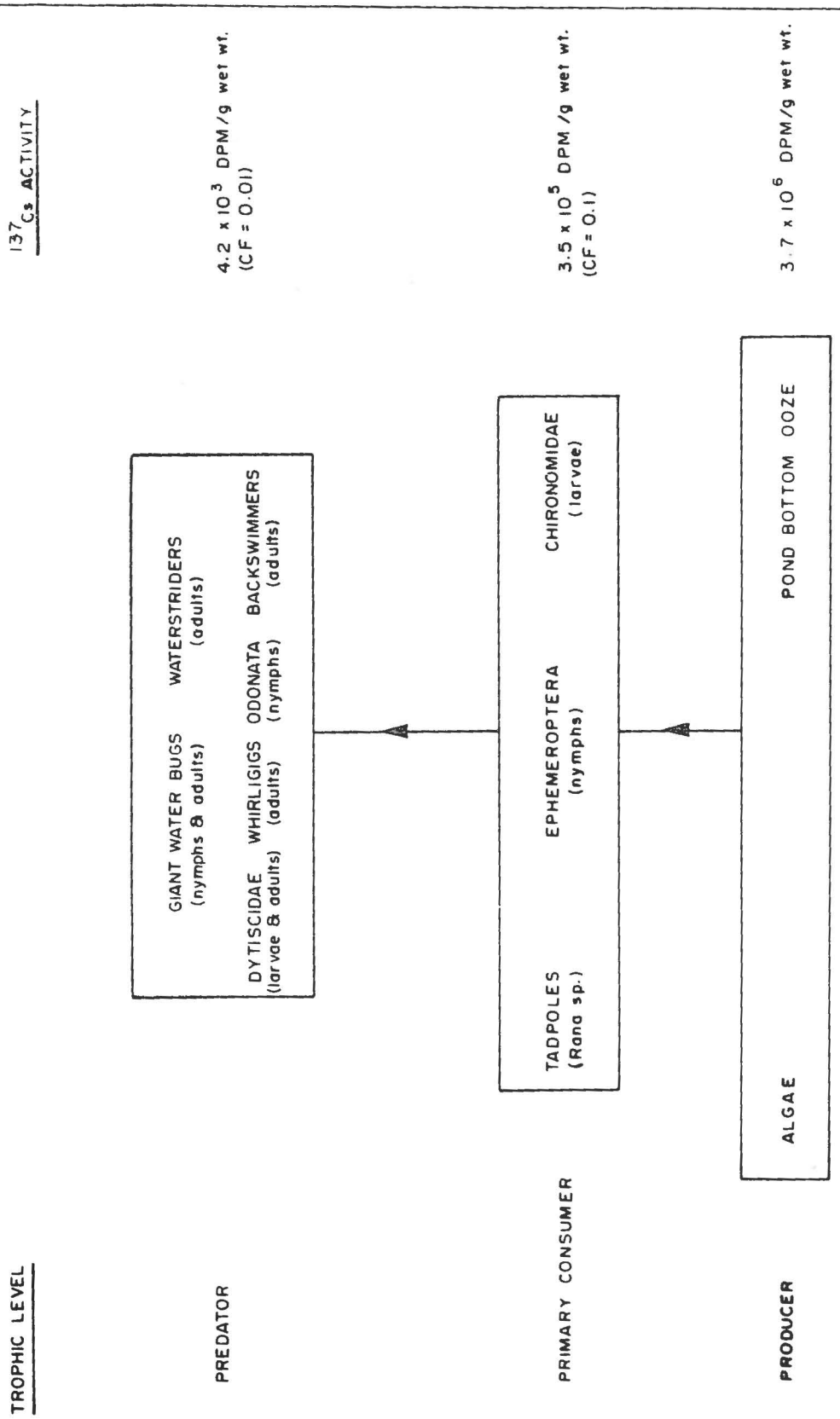

Figure 4. Stratification, based on trophic-level and ^{137}Cs activities, of insects collected from the Active pond in 1967.

Food assimilation measurement employing a radioactive tracer must of necessity be based on a knowledge of the rate at which the organism eliminates the tracer. The insect is fed a labelled food source. After a suitable level of radioactivity has been accumulated, the insect is fed unlabelled food and the rate of elimination of the tag is determined. From this measurement and a knowledge of the specific activity of the labelled food and the steady-state body-burden of the insect, food ingestion and the amount of ingested food which is assimilated, may be calculated (see Crossley and Howden, 1961 for procedural details). Several factors must be borne in mind when using this method. Depending on the species of insect being studied and the radionuclide employed, assimilation and elimination rates may be temperature-dependant. Kormondy (1965) has reported the uptake and loss of ^{65}Zn by the dragonfly *Plathemis lydia* are independent of temperature at 10, 20, and 30C. In contrast, ^{137}Cs uptake by *Aedes aegypti* is affected by temperature (Guthrie and Burzynski, unpublished results) since accumulation by larvae was greater at 25C than at 20C. The elimination-rate may also be dependent on the instar, or on the age of the adult. Crossley (1966) found that the biological half-life of radiocesium was less for the larvae of *Chrysomela knabi* than the adult stage of this terrestrial beetle, and that newly emerged adults did not eliminate ^{137}Cs as quickly as did overwintered adults. Guthrie and Brust (1969) have reported ^{137}Cs biological half-lives of 4.5 days and 10.8 days respectively, for fourth instar and adult giant water bugs, but the age of the adults had no effect on the ^{137}Cs elimination rate. As already pointed out, food consumption calculations are based on laboratory estimations of the fraction of ingested food that is assimilated. Crossley and Howden (1961), studying insect-vegetation relationships in an area contaminated with radioactive wastes, used an assimilation fraction unity. Reichle has reported factors of 0.7 and 0.87 for the four species of terrestrial isopods which he studied (Reichle, 1967). Guthrie and Brust (1969) calculated the assimilation factor of their 4th instar water bugs, an insect equipped with piercing-sucking mouthparts, to be 1.0, but that of the adults was only 0.07. Clearly then, large differences between the ^{137}Cs elimination rates and assimilation-fractions of terrestrial and aquatic insects are to be expected.

A basic assumption of food-consumption measurements using labelled food is that the amount of nuclide acquired by the organism is representative of the amount of food ingested, implying that the label must remain fixed to the food. Studies of food consumption by mosquito larvae at WNRE have shown that enough ^{137}Cs leached into the rearing medium from the various foods which were used, to permit the larvae to accumulate a significant amount via the papillary membrane, as well as from the gut. Furthermore, although this insect accumulates radiocesium via both routes, it eliminated the nuclide through the gut only. The concentration of KCl in the rearing medium was also found to affect the rate at which the nuclide was accumulated, but had no affect on the rate at which it was eliminated.

CONCLUSION

The presence of radiocesium or its experimental introduction to an environment affords the ecologist with a unique experimental tool with which to investigate trophic-level relationships and the food-chain energetics of insects inhabitating aquatic environments. Some applications at WNRE have been described to illustrate the general methodology. Radiocesium artifically introduced into an aquatic habitat affords a means for conveniently irradiating that habitat, to investigate the significance of ionizing radiation as an ecological stress. In Canada, only a beginning has been made on this aspect of radionuclide use.

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PROCEDURES AND EXPERIMENTS IN POPULATION SUPPRESSION OF THE CODLING MOTH, *LASPEYRESIA POMONELLA* (L.), IN BRITISH COLUMBIA ORCHARDS BY RELEASE OF RADIATION STERILIZED MOTHS

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ABSTRACT

Procedures are briefly described for the experimental control of the codling moth in British Columbia apple orchards by the release of gamma irradiated moths. The procedures include: preparing the orchards for moth release; estimating the wild population; forecasting the start and estimating the rate of adult emergence in the field; and marking and releasing the sterile moths. Experiments on control, from 1962 to 1970, are reviewed. Very good control was achieved in all experiments where fully sterile moths were released. Results in 1970 suggest that release of partially sterile males plus fully sterile females may be more effective than release of fully sterile moths of both sexes.

The codling moth, *Laspeyresia pomonella* (L.), is the most serious pest of apples in British Columbia, and indeed in most apple producing countries throughout the world. This insect has 2 complete generations per year in most fruit growing areas of British Columbia. Although it can be controlled effectively by chemical sprays, the constant use of these chemicals has created many problems such as insecticide resistance, destruction of beneficial arthropods, increased populations of phytophagous mites, and soil contamination. Classical methods of biological control, including the introduction of imported parasitic and predacious insects, and spraying with parasitic nematodes, bacteria and fungi, have been unsuccessful. However, two relatively new biological procedures, spraying with a disease-producing virus and the release of sterile moths, may eventually provide an alternative to the use of insecticides.

My paper will be devoted to the field procedures used in assessing the effectiveness of sterile codling moths in suppressing this pest, and will also review the results of field experiments from 1962 to 1970.

EXPERIMENTAL PROCEDURES

Preparing the experimental orchard for sterile moth release

The results of sterile moth release are most easily assessed if the experimental orchard is completely isolated from outside sources of reinfestation. However, such isolation is virtually impossible in British Columbia orchards. Marked male moths were recovered up to 9 km from release sites and adjacent apple orchards are very seldom that far apart. However, the moth does restrict its flight in areas that are densely planted to apple. For example, when a 4-hectare orchard in a densely planted area received 368,000 marked moths only 3 of the male moths were recovered in a sex trap 2 km away. Consequently, the limited

reinfestation that would occur in commercially operated apple plantings can be tolerated if the aim of the experiment is control rather than eradication. Nevertheless, every attempt was made to protect the experimental orchards from outside reinfestation by removing or spraying abandoned and neglected host trees within 3 km of the orchard with a persistent codling moth insecticide both before and during the course of the experiments.

The initial wild population in some of the experimental orchards was so high that it would have been impossible to produce sufficient moths in our limited rearing facilities to overflood the wild insects with sterile moths. In these orchards the wild population was first reduced to manageable levels by applying chemical sprays, or by picking the fruit from the trees, one year before starting the release program.

Estimating the wild population

The numbers of moths that must be reared in the laboratory to overflood the wild population in the orchard at a predetermined ratio depends largely, though not exclusively, on the size of the wild population. The numbers of codling moths likely to be present in spring were estimated by examining a known percentage (at least 10%) of the fruit at harvest for larval exit holes. Each hole was taken as representing a mature diapausing larva potentially capable of overwintering. (A small proportion of the mature larvae from the previous (1st) generation would have entered diapause and would be able to overwinter, but the numbers were considered too small to include in the estimate). The numbers of overwintering larvae that die without reaching the adult stage must be deducted from the total numbers of larvae that entered diapause, but at present the information required to make an accurate estimate of this mortality is unavailable. We know that insectivorous birds and the hymenopterous parasite *Ascogaster quadridentata* Wesmael frequently destroy 50% or more of the diapausing larvae in unsprayed and abandoned orchards, whereas in sprayed orchards predators and parasites are of little importance. Unusually severe winters cause great mortality in diapausing larvae, particularly where there is a light snow cover. In 1968, for example, winter temperatures in many British Columbia orchards fell to -30° C and lower, resulting in considerable larval mortality and in below normal codling moth infestations the following summer. For the present, until more detailed data are accumulated, we rather arbitrarily assume about 20% overwintering mortality in commercial orchards and 50% in abandoned orchards, but these percentages must be increased in unusually cold winters.

Forecasting the start and estimating the rate of adult emergence

A procedure was needed to forecast the commencement date of adult emergence in spring so that some sterile moths could be released just before this event. The use of so-called heat units (Glenn 1922) or developmental units (Shelford 1927), to forecast the date of emergence was not as accurate as might be expected from some of the published literature. However, we were able to relate adult emergence to apple bud development; eclosion was found to start at the late pink-bud stage of the McIntosh variety.

The commencement and rate of adult emergence in spring was at first determined by frequent examination of natural and artificially-provided cocooning sites for empty pupal cases. An improvement in this procedure was later adopted. In autumn, known numbers of field-collected diapausing larvae were caged at various locations on the tree, both above and below soil level. Larval mortality was determined early in spring and thereafter adult emergence was recorded daily so that the commencement and rate of emergence could be easily established. Over a number of years it was found that the peak of eclosion occurred about 3 or 4 weeks after the late pink-bud stage of apple development. This information, used in conjunction with temperature records in the orchard and graphs of moth flight in previous years, now allows us to forecast the date of peak eclosion in spring to within about one week of the actual event.

The rate of adult emergence during the second generation was established by the use of female-baited sex traps coupled with temperature records and graphs of moth flight from previous years.

Releasing the sterilized insects

The method of release should in itself distribute the sterile moths uniformly throughout the orchard for in densely planted orchard areas the codling moth, particularly when both male and female moths are released together, tends to remain rather close to the point of release.

Ground release stations were used in the early experiments. The most satisfactory type was a shallow box in which 3 of the sides were made of wire screen. The screen kept out insectivorous birds but did not impede the moths from leaving the box. A hinged plywood lid gave protection from rain. Twelve boxes per hectare was an adequate number for satisfactory moth dispersal (Proverbs *et al.* 1969).

The use of fixed ground release stations was too slow for distributing moths in large orchards. Consequently, in 1969, the moths were dropped in cardboard boxes from a low-flying helicopter using a procedure developed by the U.S. Department of Agriculture (Butt 1967). Each hectare received about 11 boxes of moths. The release procedure was speeded up and improved in 1970 by discharging the moths from the helicopter without the protection of boxes or other containers. The cold-immobilized moths were fed into a discharge tube via a rapidly vibrating trough, the rate of moth discharge being directly proportional to the rate of trough vibration.

A ground release system was also developed in which the moths were fed through a vibrating trough into the air stream of a small electric fan mounted on a tractor. This system might be used in areas that are inaccessible to aircraft.

The efficiency of the last two methods was compared to a previously used procedure in which moths contained in open paper bags were thrown from a truck driven slowly through the orchard. The percentage of male moths recovered in sex traps (the moths were marked differently for each type of release) was 51 for the paper bag method, 46 for the helicopter procedure, and 44 with the tractor-mounted air fan, indicating that the three procedures were about equally effective as far as moth survival was concerned.

In 1971, tests will be conducted to determine if the moths can be released without damage from fixed wing aircraft. The use of such aircraft would appreciably reduce the costs of releasing the insects, which, at present, is one of the most expensive operations in codling moth control by the sterility technique.

Marking the sterilized moths

All sterile moths destined for release were marked so that, with the aid of traps, a more or less continuous record could be kept on the ratio of sterile to wild moths in the orchards. The longevity and rate of dispersal of the sterile insects could also be established where different color markers were used successively throughout a period of several releases.

A number of marking procedures were tried including spraying the moths with alcoholic or acetone solutions of eosin, dusting the moths with zinc 8-hydrozyquinoline (this chemical fluoresces strongly in ultra violet light), and the use of the so-called golden strain of codling moth (Essig 1939) as a genetic marker. The presently used procedure consists in dusting the adults with Day-Glo pigments (Switzer Bros. Inc., Cleveland, Ohio, U.S.A.) which are available in several colors and are fluorescent under ultra violet light. These pigments do not measurably affect longevity, mating, or egg-laying, but will cause some reduction in the response of the male to untreated virgin females if too much pigment is applied. Another disadvantage of Day-Glo may appear where large numbers of moths are captured in sex traps. Small amounts of the pigment may be transferred from treated to untreated adults which could result in misidentification of fertile wild moths.

EXPERIMENTS ON CONTROL

Ground release of males alone in an abandoned orchard

In 1962, in this first experiment on control (Proverbs *et al.* 1966), the insects were sterilized as pupae and only male moths were released. The test orchard consisted of 20 abandoned apple trees which were severely infested with codling moth every year. Because

of the high infestation the numbers of moths were first reduced to manageable levels by spraying with DDT one year before the release of sterile insects. Virtually complete sterility was induced in the insects by exposing the pupae about two hours before eclosion, in a ventillated canister at about 15°C, to 40 krad of gamma radiation from Co^{60}. The male moths were marked with a fluorescent dust and equal numbers released from each of 20 stations, 1 station per tree. In this, and in all subsequent experiments, the first release every year was made at the early pink-bud stage of McIntosh apple and the last release in late September when moth flight had virtually ceased. Releases were made three times per week. As a rule, the numbers of moths released on any specific day were adjusted to the rate of adult eclosion in the field in order to maintain a ratio of at least 20 sterile males to 1 fertile (wild) male.

After the first year of release, examination of windfall and harvested fruit showed that the moth population had increased to 957 diapausing larvae from an estimated 400 larvae the previous autumn. This increase was attributed to an insufficient number of sterile moths during peak eclosion of the wild first brood adults. During this period there was a sudden reduction in the supply of moths from the rearing facility because of an unforeseen shortage of apples for larval rearing. Sex trap records from the orchard indicated that the ratio of sterile to fertile (wild) males at this time was about 8:1 instead of the intended ratio of at least 20:1 which previous field cage tests had indicated to be necessary for rapid suppression of codling moth reproduction.

During the second year of the program larger numbers of sterile moths were released, particularly during peak emergence of the first brood adults. Results were much more encouraging for fruit examination at harvest indicated that only about 43 mature larvae were present in the orchard.

During the third year of the experiment more than 2000 male moths were trapped but only 1 of these was a wild male. And at harvest, only 6 apples had exit holes from 2nd generation larvae. Complete elimination of the codling moth might have been achieved if the test orchard had been completely isolated from outside sources of reinfestation.

Ground release of moths of both sexes in an abandoned orchard

In the second experiment on control (Proverbs *et al.* 1967) the insects were irradiated as adults and moths of both sexes were released. This procedure was adopted because too much time had to be spent sexing and sorting mature pupae for irradiation. The adult moths were irradiated, usually 1-48 hr after emergence, in a carbon dioxide atmosphere at about 13°C. The irradiation dose used, 50 krad, induced about the same degree of sterility as the 40 krad dose delivered to aerated pupae in the previous experiment.

The experiment was conducted in an abandoned 2-hectare apple orchard with a history of severe codling moth injury. However, one year before starting the experiment the high codling moth population was reduced to a manageable level by picking and destroying most of the infested fruit. The sterile moths were marked and released as described in the first experiment.

One year after releasing sterile moths the numbers of diapausing larvae at harvest had been reduced to about 119 from an estimated 5000 the previous autumn. One year later, following further moth releases, the numbers of diapausing larvae had further declined to 55, which represented 0.09% damaged fruit. Control might have been even better if reinfestation could have been avoided from abandoned apple trees 1.5 km away.

Because of many uncontrollable variables, critical comparison cannot be made between the results of this experiment, in which moths of both sexes were released, and the results of the first experiment in which only males were released. Both procedures gave good control, but there is some concern that where moths of both sexes are released, the sterile males may mate with nearby sterile females rather than seek out fertile wild females that may be further away.

Ground release of moths of both sexes in a commercial orchard

Although the two previous experiments showed that sterile insect release would control the codling moth in abandoned orchards, information was needed on the effectiveness of this method in commercially operated orchards in which the usual cultural operations and spray programs (with the exception of codling moth sprays) were followed.

A 4-hectare commercial apple orchard, under good codling moth control, was selected (Proverbs *et al.* 1969). Moths of both sexes were sterilized by exposures to 50 krad in a carbon dioxide atmosphere at about 17° C marked, and released from ground stations 3 times weekly as in the previous experiments. During the first year of the experiment moths were released in 1.3 hectares and the remaining 2.7 hectares were sprayed with an effective codling moth insecticide. At harvest time, only 3 injured apples were found in the release area whereas approximately 0.5% of the fruit was damaged by codling moth in the sprayed section, that is, about the same level of injury recorded the previous autumn.

The exceptionally good control achieved during the first year of release was due to the maintenance of a high ratio of sterile to fertile males. The average for the season, on the basis of sex trap records, was 280:1, and the minimum about 17:1 for a 7-day period. During the second year of the experiment the ratio was allowed to drop to about 10:1 during the peak of emergence of the first brood moths. Small numbers of larval entries were soon observed in the apples, indicating that a 10:1 ratio of sterile to fertile males was not quite high enough to maintain control even at this time of the year when inclement weather keeps the reproductive rate of the codling moth at a modest level. During the second brood the ratio was again permitted to decline to about 10:1, and very shortly after this new larval entries were readily observed. The ratio was immediately increased to about 40:1 and maintained at this level for the rest of the season. Fruit injury at harvest was 0.1%. The results, coupled with those of an earlier experiment, suggest that a ratio of about 20 sterile to 1 fertile male may be required to keep a codling moth population from increasing, and that this ratio may even have to be increased when weather conditions are particularly favorable for codling moth reproduction.

Two-thirds of the orchard had to be sprayed during the third year of the experiment because of an accidental release of inadequately sterilized moths in July. At harvest 0.7% of the fruit was found to be injured by the codling moth in the unsprayed area but most of the injury was caused by the progeny of fertile adults released in July.

In the second and third years of the experiment, when sterile moths were released in the entire 4-hectares, trapping records indicated that 12 ground release stations per hectare was an adequate number to ensure rapid and reasonably uniform dispersal of the released insects.

Aerial release of moths of both sexes in a commercial orchard

The previous experiment indicated that the sterility method of control was effective in commercial orchards subjected to commonly used pesticide programs. However, more rapid procedures were required for releasing the sterile moths, and information was needed on the effectiveness of moths produced on an artificial diet for up to this time all experiments had been conducted with apple-reared moths.

A 40-hectare commercial apple orchard was selected. Moths, 90% of which were reared on an artificial diet (Brinton *et al.* 1969), were chilled to about 5°C. and then exposed to 50 krad in a carbon dioxide atmosphere. After the moths were marked they were packed into small cardboard boxes and released in the boxes from a helicopter as described earlier. As in the other experiments, the moths were released 3 times weekly starting at the early pink-bud stage of apple and discontinuing in late September when moth flight had ceased. The ratio of sterile to wild males was kept at or above 35:1 except during the first two weeks of release when the ratio was 5:1.

The aerial release method, and the artificial diet-reared moths, evidently performed very well for fruit examination at harvest showed that only 0.05% of the apples were injured by codling moth, a level of injury well below that in surrounding sprayed orchards.

Release of partially sterile male plus fully sterile female moths

Some years ago (Proverbs and Newton 1962) it was shown in the laboratory that when the male codling moth was exposed to certain sterilizing doses of radiation and then crossed with non-irradiated females, the surviving offspring were mostly males and these males were largely sterile. The F_1 females were completely sterile. These findings were not followed up by field experiments because it was feared that although most of the F_1 larvae would die during development too many of them would injure the fruit before they succumbed. However, because of the poor competitiveness of fully sterile moths and because of the high costs of laboratory rearing, it was decided in 1970 to reassess the possibility of using partially sterile males plus fully sterile females in control programs.

Laboratory and field cage trials indicated that partially sterile male moths were indeed more competitive than fully sterile moths. For example, in one trial moths were chilled to about 7°C and exposed in a carbon dioxide atmosphere to 30 or 50 krad. (Under these conditions 50 krad males x non-irradiated females results in about 2% egg hatch and 30 krad males x non-irradiated females in about 10-15% hatch). The irradiated moths were introduced into caged apple trees with non-irradiated insects at a ratio of 15 irradiated male and female moths to 1 untreated male and female. When the F_1 offspring had completed development, it was found that cages which initially contained 50 krad moths had produced 1.7 times as many F_1 adults as the cages with 30 krad moths.

In 1970, the orchard that was used in the last field experiment was divided into 2 blocks, 36 hectares to the north and 4 to the south. Three times weekly fully sterile male plus female moths (exposed in air to 40 krad) were released by helicopter in the north block and partially sterile males plus fully sterile females (25 krad exposure) in the south block. Fruit examination at harvest is not yet complete but the results to date (October 30) indicate that codling moth has injured about 0.01% of the apples in the block where sterile moths were released and 0.08% where partially sterile males plus fully sterile females were liberated. However, this does not mean that control in the latter was inferior. The rate of moth release throughout the season was approximately the same in the 2 blocks, but the infestation last autumn was much higher in the south block than in the north. At that time the percent injured fruit in the latter averaged approximately 0.05 whereas in the southwest corner of the south block injury was 1.0%. Furthermore, in 1970, most of the injury recorded at harvest in the south block actually occurred in early summer, that is during the first brood. Consequently, reproduction in the south block in 1970 was evidently suppressed, particularly in the second brood, much more effectively than indicated by the 0.08% injury recorded. One encouraging feature of the experiment was the complete lack of stings or superficial fruit injury. Larval offspring of 25 krad males x wild females were evidently so weak that they were unable to feed on the apples under field conditions.

Partially sterile males plus fully sterile females (25 krad dose) were also released in two small abandoned apple orchards. The number of irradiated moths released per tree was approximately the same in each orchard during the first brood, but during the second brood the number released per tree in one orchard was about twice that in the other. At harvest 0.6% of the fruit was injured by codling moth where the smaller numbers of moths were released and 0.1% where the larger numbers of moths were liberated. The former orchard was probably invaded by fertile moths from neighbouring semi-neglected apple trees. Also, some of the injury attributed to codling moth in this orchard may have been due to *Grapholitha prunivora* (Walsh). The codling moth infestation in this orchard is about the same as it was the previous autumn after 3 codling moth sprays. In the other orchard, which was subjected to very little reinfestation, the 0.1% injury was about one-tenth of that recorded the previous year when chemical sprays were applied.

The release of partially sterile males plus fully sterile females has given promising results but further work is needed to assess the effectiveness of this procedure more precisely. In view of the absence of stings in the field trials it may be feasible to reduce the exposure dose below the 25 krad level used in 1970.

POPULATION DENSITY OF SOME APPLE PESTS AFTER RELEASING STERILE CODLING MOTHS

The following observations on pest density were made in two commercial apple orchards subjected to 2- and 3-year programs of sterile codling moth release.

The apple aphid, *Aphis pomi* De G., and the woolly apple aphid, *Eriosoma lanigerum* (Hausm.),which are sometimes troublesome pests in sprayed orchards, were of no economic importance. The European red mite, *Panonychus ulmi* (Koch), which is one of the most injurious spider mites in British Columbia apple orchards, remained at noninjurious levels in one orchard; in the other, one chemical spray had to be applied in each of three consecutive years. The McDaniel spider mite, *Tetranychus mcdanieli* McG., an injurious species in sprayed orchards, was of no significance in one orchard. In the other orchard, it built up to damaging numbers in the first year so that one miticide spray had to be applied; in later years it was held in control by predators, particularly *Typhlodromus occidentalis* Nesbitt. Every year rust mites were found in the orchards but no special treatment was required for control. The fruit tree leaf roller, *Archips argyrospilus* (Walker), which was one of the most serious apple pests in British Columbia prior to the introduction of the codling moth, increased fairly rapidly necessitating the application of an insecticide in both orchards during the second year of the release programs. The eye-spotted bud moth, *Spilonota ocellana* (D. & S.), and the white apple leafhopper, *Typhlocyba pomaria* McAtee, two serious apple pests in this fruit-growing area, did not increase as anticipated. Chemical sprays were not specifically required against these pests during the 2- and 3-year programs of sterile moth release.

Results to date show that the codling moth can be controlled in British Columbia by the release of sterile moths. Many improvements can be made in the presently used techniques, but the over-riding consideration now is to determine whether the method is economically feasible on an area wide basis.

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POPULATION CONTROL OF LEPIDOPTERA: THE GENETIC AND PHYSIOLOGICAL BASIS

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INTRODUCTION

Many research workers have been trying to emulate the success of the sterile male release program with the screwworm fly, *Cochliomyia hominivorax* (Coquerel), with sterilized Lepidoptera (Bushland 1970). These efforts have not proved nearly as successful as those with the Dipteran species. The only release of sterile moths to achieve population control that can be enthusiastically cited to date has been recorded by Proverbs *et al.* (1969) and Proverbs (1970). These authors released sterile male codling moths, *Laspeyresia pomonella* (L.), over a period of 3 years in a commercial orchard in the Okanagan Valley in Canada. The results of these releases appear promising since good control was obtained for 4 years.

Lepidopterous insects include some of the most destructive pests in agriculture. The need for a successful means of biological control has become increasingly more urgent with the mounting concern over insecticide use. The approach to date has been primarily the release of sterile moths into the natural population.

The largest single drawback in the use of radiation-sterilized male moths to control natural populations of lepidopterous insects has been the inability of the irradiated males to compete successfully with natural males. North and Holt (1968a) pointed out that the reason for the lack of competitiveness of radiosterilized cabbage loopers, *Trichoplusia ni* (Hubner), was the inability of irradiated males to transfer sperm successfully. Irradiated male Lepidoptera mated to unirradiated females often fail to elicit a normal ovipositional response. This has been reported by many workers (Godwin *et al.* 1964, Ouye *et al.* 1964, Raun *et al.* 1967, North and Holt 1968a, Flint and Kressin 1969, Cheng 1969, and Chawla *et al.* 1970). *Heliothis zea* has been shown to be an exception to this (North and Holt 1970a) in that sperm transfer is not reduced at the sterilizing dose. However, the exact relationships involving sperm transfer to the female and the elicitation of the oviposition response are not presently clear. The inability of the irradiated male cabbage looper to transfer sperm that will reach the spermatheca is dependent on the dose of radiation received (North and Holt 1968a).

The routine experimental procedure to determine the mating ability of treated moths has involved dissecting the female bursa copulatrix and counting the spermatophores. Taylor (1967) pointed out the fallacy of assuming a direct correlation between the presence of a spermatophore and the transfer of sperm; he showed that male *Atteva punctella* (Cramer) may transfer spermatophores without transferring sperm. This was also pointed out for the cabbage looper by North and Holt (1968a) and for the tobacco budworm, *Heliothis virescens* (F.) by Flint and Kressin (1969); and George and Howard (1968) indicated that after continued mating, males of the oriental fruit moth, *Grapholitha molesta* (Busck), are capable of transferring sperm successfully without transferring a spermatophore. Therefore, it is evident that assaying for a spermatophore is not a sound technique to determine sperm

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transfer. The procedure that has evolved is the dissection of the bursa copulatrix (to determine the presence of a spermatophore) and the dissection of the spermatheca (to determine the presence of sperm). This is usually done after the completion of oviposition by the female and is often misleading in terms of the type of sperm present. The successful mating of the cabbage looper (and presumably other Lepidoptera) requires the incorporation of both eupyrene and apyrene sperm in the spermatophore bulb, the positioning of the stalk at the opening of the seminal duct, and the movement of the sperm from the spermatophore bulb to the spermatheca via the seminal duct and common oviduct (Holt and North 1970). An unsuccessful mating occurs when any one of these criteria is not met.

Taylor (1967) noted that the occasional failure of *Atteva punctella* (Cramer) to transfer sperm in mating is rather common, even when the male is not irradiated. North and Holt (1968a) observed this to be true with unirradiated pair matings of the cabbage looper in particular with the first mating of a 1-day-old male. Therefore, the condition that results in unsuccessful sperm transmission by irradiated male moths also exists, but to a lesser degree, in normal untreated insects.

It has become evident that duplication of the procedures used for sterile male releases with dipteran species are not directly applicable to controlling Lepidoptera. This does not imply, as some would suggest, that the technique is of no value in controlling lepidopterous species. It means, however, that researchers must develop modifications and apply techniques based on the biological uniqueness of Lepidoptera.

Proverbs (1962) first noted that the progeny of irradiated codling moths were sterile. Cogburn *et al.* (1966) said the progeny of irradiated Indian meal moths, *Plodia interpunctella* (Hubner), and the Angoumois grain moth, *Sitroga cerealella* (Olivier) were also sterile. North (1967) and North and Holt (1968a and 1968b) demonstrated the same phenomenon in the cabbage looper, *Trichoplusia ni* (Hubner), and found complex chromosomal rearrangements to be the probable primary cause of the inherited sterility; they suggested the use of this type of sterility for control of lepidopterous populations. Bauer (1967) has described the genetic behavior of chromosome translocations in *Pieris brassicae* L. Since then, inherited sterility has become an accepted phenomenon in Lepidoptera; it has been found in 11 other species.

The phenomenon of inherited sterility is unique to Lepidoptera, Hemiptera, and Homoptera in that species of these orders have holokinetic chromosomes. Species having this particular chromosome structure are resistant to radiation since induced fragmentation of the chromosomes does not lead to dominant lethality. This is one of the biological uniquenesses of Lepidoptera which can be drawn upon to modify the male-sterile technique and obtain control.

North and Holt (1969) reported that in laboratory populations of the cabbage looper, a single release of partially sterile males gave 92% control over 2 generations. Knipling (1970) thoroughly discussed releasing partially sterile moths to achieve population suppression. He projected moth population trends under various release schemes. Research has been continued to determine the most efficient way to achieve inherited sterility in Lepidoptera.

The Effect of Radiation on the Ability of Male Moths to Transfer Sperm

The reproductive systems of Lepidoptera are similar, but variation does occur in size, shape, and placement of the female accessory organs. In almost every species there is a differently shaped bursa copulatrix, and there is a distinctive variation in the size and shape of the spermatophores.

Callahan and Chapin (1960), in their study of the comparative morphology of 3 noctuids, noted that there is some evidence that certain specimens are more likely to successfully complete the mechanics of copulation than are others. The number of unsuccessful matings appeared to be directly correlated with the complexity of spermatophore inversion. Callahan reported 2.8% aberrations in matings of untreated corn earworms, *Heliothis zea* (Boddie), 0% in the variegated cutworm, *Peridroma saucia*

(Hubner), and 15.5% in the armyworm, *Pseudaletia unipuncta* (Haworth). A number of aberrations in matings for this last species were attributed to the complexity of the spermatophore insertion as opposed to 0.0% in the variegated cutworm. North and Holt (1968a) reported 22% aberrations for singly mated untreated male and female cabbage loopers; Flint and Kressin (1969) reported 15% aberrations of sperm transmission in the untreated tobacco budworms. Studies of the reproductive tracts of the cabbage looper, tobacco budworm, and the corn earworm and a comparison of the diagrammatic illustrations of the three species mentioned in the literature cited above reveal considerable variation in the endophallus and cuticular lower simplex between males; they also reveal considerable difference in bursa copulatrix among females. These variations in males of various lepidopterous species offer some explanation of the variation in sperm transfer under normal conditions and after irradiation.

As shown by Holt and North (1970), the irradiated male cabbage looper does not really fail to transfer sperm but because of a disruption in the timing of the mating process, the sperm of the irradiated male are ejaculated directly into the bursa copulatrix rather than incorporated into the bulb of the spermatophore. They pointed out that though only a small percentage of the males actually have a normal complement of sperm incorporated in the spermatophore bulb, when the total sperm count of the ejaculate is considered (whether it fills the spermatophore or is placed into the bursa copulatrix) the number of sperm ejaculated for both control and irradiated males is the same. This means that when irradiated males transfer sperm, the placement of the sperm becomes the all-important factor.

Holt and North (1970) also pointed out that the eupyrene sperm of the cabbage looper, which are nucleate and capable of fertilization in contrast with the anucleate apyrene sperm (Riemann 1970), do not become motile until they have reached the spermatheca of the female. Therefore, any eupyrene sperm placed directly into the bursa copulatrix cannot find their way up the seminal duct. On the other hand, since apyrene sperm possess motility when incorporated into the ejaculate, they can find their way to the spermatheca by random chance. This explains why irradiated males often appear to transfer only apyrene sperm.

If radiosterilized males (at least in some species of Lepidoptera) are to be used in a release program for population control, a way must be found in a large percentage of cases for irradiated males to transfer successfully a normal complement of eupyrene and apyrene sperm to the female. This becomes important in a polygamous species because an irradiated male in mating with a previously mated female must be capable of displacing the original sperm in the spermatheca. If this does not occur, the irradiated male mating would be totally ineffective. Mating competitiveness in Lepidoptera may well be a problem of sperm competition and, possibly even more important, a problem involving the quantity of sperm as it relates to matings by unirradiated and irradiated males.

This paper discusses the two basic aspects of sperm competition: (1) whether a particular stage and type of radiation is more advantageous in obtaining better sperm transfer or sperm utilization; and (2) the effect that sperm transfer *per se* or related accessory fluids have on the ovipositional response elicited in the female.

Sperm Transfer by Irradiated Males

The sperm transferred in the cabbage looper and the corn earworm during mating are those stored in the duplex regions of the male reproductive tract; cabbage looper males are not ready for mating until they are 2-3 days old, whereas corn earworm males are ready when 1 day old.

The most important aspect of sperm transfer is the type of sperm transferred. Apyrene sperm are anucleate and therefore incapable of fertilization. In most species they are smaller but more motile than eupyrene sperm (Iriki 1941), but in the armyworm the apyrene are considerably larger than the eupyrene sperm (Holt and North, unpublished). Eupyrene sperm are nucleate and undergo (at least in the cabbage looper and probably in other Lepidoptera) gross morphological changes during spermiogenesis from the time they leave the testes until they reach the spermatheca (Riemann 1970).

The irradiated corn earworm is an example of a Lepidopteran with no apparent problem in sperm transfer. A comparison was made (Table 1) of the ability of unirradiated and irradiated 3-day-old male cabbage loopers and corn earworms to transfer successfully sperm when allowed to mate for 3 nights. The greatest difference was in the percentage of males able to transfer a normal ratio of eupyrene:apyrene sperm. The cabbage looper male, even though allowed to mate for 3 nights, failed to transfer sperm successfully as the radiation dose increased; 100% of the corn earworm males that mated transferred a normal ratio of eupyrene:apyrene sperm (even at 25 krad). Apparently the irradiated corn earworm should be competitive, both from a standpoint of mating and ability to transfer sperm, when placed with unirradiated males. We therefore conclude that the release of sterile corn earworm males is more promising than the release of sterile cabbage looper males for population suppression.

The reasons for the irradiated cabbage loopers not transferring eupyrene sperm were discussed by Holt and North (1970). When sperm are deposited in the bursa copulatrix by an irradiated male, the eupyrene sperm are immobile and cannot get to the spermatheca, but the apyrene sperm apparently can. Examination shows the females have sperm, but when the males received high doses of radiation, very few females received sperm capable of fertilization.

To test the effect the number of matings had on sperm transfer by irradiated male cabbage loopers, experiments were conducted where 3-day-old males were mated consecutively for 8 nights (Table 2). A large percentage of the control males failed to transfer a normal ratio of eupyrene:apyrene sperm the first night, but after the first night they maintained a normal percentage. Males that received 5 krad of radiation transferred sperm as well as the controls. However, males that received 15 krad showed a definite reduction in the percentage of individuals that transferred a normal ratio of eupyrene:apyrene sperm. These males reached their peak between the 4th and 6th matings. This is probably the reason that in competitive tests reported by North and Holt (1969) males given 15 krad were competitive. Males receiving a sterilizing dose of 30 krad showed a greater ability to transfer a normal ratio of eupyrene:apyrene sperm in the first two matings than they did thereafter. It is generally true in other tests with the cabbage looper that a male that failed to transfer a normal complement of sperm in the first several matings rarely recovered this ability. This means that in multiple matings a sterile male would not be able to compete effectively with unirradiated males. It is expected that during the first night of mating a sterile male would compete with unirradiated males simply because the latter often fail to transfer sperm during the first mating.

The Ability of the Cabbage Looper Males Irradiated as Pupae to Transfer Sperm Successfully

There are many economic advantages in irradiating pupae rather than adults, but pupal irradiation has not proved successful in producing competitive males (Proverbs and Newton 1962, Flint and Kressin 1967, Cheng 1969). Male pupae were irradiated with various doses of gamma radiation 5 days before emergence. The ability of the resulting adult male moth to mate and transfer sperm is shown in Table 3. These data show (1) that the percentage of males that mated decreased rapidly as the radiation dose increased, and (2) at the sterilizing dose (20 krad) only 8.3% of the males tested mated and none of these mated males transferred sperm. This clearly shows that the percentage of sterility resulting from radiation of pupae at this stage with gamma radiation is the same as that of aspermia. Even at relatively low doses (10 krad), only 7.1% of the males transferred a normal ratio of eupyrene:apyrene sperm. Irradiation of cabbage looper pupae therefore does not produce very competitive sterile insects.

Studies were done to determine whether the type of radiation used on pupae had any bearing on the production of competitive males. Pupae were irradiated 5 days before emergence with various doses of 0.43 MeV fast neutrons, and the ability of the resulting adult males to transfer sperm was studied (Table 4).

TABLE 1.

The effect of gamma radiation on the ability of 3-day-old adult male moths of *Trichoplusia ni* and *Heliothis zea* to successfully transfer sperm (♂♂ allowed to mate 3 nights).

Dose of gamma radiation to 3-day-old ♂♂ (krad)	% Males mated		% Mated males transferring sperm		% of males transferring normal ratios of eupyrene:apyrene sperm	
	T. ni	*H. zea*	*T. ni*	*H. zea*	*T. ni*	*H. zea*
0	70.7	80.0	88.0	75.0	78.0	100.0
5	66.1	85.7	87.4	80.0	63.5	100.0
10	—	71.4	—	100.0	—	100.0
15	68.5	85.7	80.6	100.0	42.7	100.0
20	—	80.0	—	75.0	—	100.0
25	—	85.0	—	100.0	—	100.0
30	66.9	—	64.7	—	13.7	—

TABLE 2.

The relationship of 8 consecutive matings and the ability to transfer sperm by unirradiated and irradiated adult male cabbage loopers (♂♂ were 3 days old at beginning of test).

Number of consecutive matings	Number of of individuals	% Mating	% ♂♂ mated transferring sperm	% ♂♂ that transferred normal ratio eupyrene:apyrene sperm
		Unirradiated males		
1	56	85.7	64.6	32.3
2	58	77.6	97.8	84.1
3	53	69.8	94.6	71.4
4	38	73.7	100.0	75.0
5	43	72.1	71.0	77.3
6	43	48.8	100.0	80.9
7	39	71.8	96.4	77.8
8	35	57.1	95.0	100.0
		Males that received 5 krad		
1	58	79.3	67.4	71.0
2	57	64.9	91.9	76.5
3	56	71.4	97.5	71.8
4	38	78.9	100.0	73.3
5	56	64.3	77.8	35.7
6	51	41.2	90.5	—
7	44	68.2	93.3	50.0
8	35	60.0	90.5	89.5
		Males that received 15 krad		
1	60	78.3	61.7	17.2
2	60	58.3	77.1	44.4
3	58	70.7	95.1	43.6
4	36	72.2	100.0	—
5	54	59.3	71.9	60.9
6	52	36.5	100.0	63.2
7	40	42.5	70.6	25.0
8	28	35.7	80.0	50.0
		Males that received 30 krad 1/		
1	60	81.7	34.7	35.3
2	58	79.3	69.6	25.0
3	56	69.6	89.7	8.6
4	38	63.2	83.3	5.0
5	44	70.5	74.2	13.0
6	41	61.0	56.0	0.0
7	40	50.0	55.0	9.1
8	35	42.9	60.0	0.0

1/ 30 krad is sterilizing dose to adult males.

TABLE 3.

The relationship of gamma radiation to the ability of 3-day-old adults to mate and transfer sperm over a 3-day period when irradiated as pupae 5 days before emergence (♂♂ allowed to mate for 3 nights).

Dose (krad)	% Mated	% ♂♂ tested transferring sperm	% ♂♂ tested transferring normal ratio of eupyrene:apyrene sperm
0	75.0	75.0	58.3
5	69.2	69.2	61.5
10	42.9	7.1	7.1
15	22.2	22.2	11.1
20 1/	8.3	0.0	0.0
25	14.3	0.0	0.0

1/ This is considered a sterilizing dose.

TABLE 4.

The relationship of dose of 0.43 MeV fast neutrons on the resulting 3-day-old adult male cabbage loopers when irradiated as pupae 5 days before emergence (♂♂ allowed to mate for 3 nights).

Dose of gamma radiation (krad)	Number of individuals tested	% ♂♂ mated	% ♂♂ tested transferring sperm	% ♂♂ tested transferring normal ratio of eupyrene:apyrene sperm
0	22	86.4	81.8	81.8
1	18	94.0	88.9	77.8
3	21	95.0	95.2	95.2
5	20	75.0	55.0	50.0
10	25	56.0	52.0	52.0
15 1/	25	60.0	44.0	36.0
20	28	28.6	17.9	10.7
25	13	7.7	0.0	0.0
30	23	21.7	6.7	0.0

1/ The average percent fertility of these males is 7.0% and can be considered the sterilizing dose.

The percentage of the males that mated decreased with the increase in dose as was found when gamma radiation was used. But when compared with the pupae irradiated with gamma radiation, the decrease was not as severe. Also, the percentage of males transferring a normal complement of sperm was high. Thirty-six percent of the males irradiated with 15 krad as pupae transferred a normal ratio of eupyrene:apyrene sperm as compared with none of the males irradiated with a sterilizing dose of gamma radiation. When pupae received a sterilizing dose of fast neutrons, only 60% of the resultant males mated but there was still a sufficient number that transferred a normal complement of sperm; this was not true when adult males were given a sterilizing dose of gamma irradiation (Table 1). The advantages of using fast neutrons in insect sterilization have not yet been fully explored. Since these data appear encouraging, the authors plan more research on the use of neutron irradiation of Lepidoptera.

The Type and Quantity of Sperm Transferred as Related to the Ovipositional Response in the Cabbage Looper

Irradiated males of many species of Lepidoptera often fail to elicit a normal ovipositional response from unirradiated females. The reason may be related to sperm transfer *per se*, or to the accessory secretion of the male. If a male fails to transfer sperm, he may therefore fail to transfer the needed accessory fluid to elicit a normal ovipositional response. Leopold (1970) in his studies on the house fly, *Musca domestica* L., showed that a basic protein in the accessory secretion of the male is probably responsible for eliciting the ovipositional response in the female. Holt and North (1970) showed that though irradiated male cabbage loopers transferred spermatophores, they often fail to transfer sperm and accessory secretions in which the sperm are embodied. Perhaps this secretion is responsible for eliciting the ovipositional response in the female cabbage looper. Tests were conducted to determine whether sperm *per se* or a particular type of sperm were responsible for eliciting the ovipositional response. Unirradiated 3-day-old males and females of the same age were mated. The females were allowed to oviposit for 2 nights, the spermathecae were dissected, and the amount and type of sperm were recorded. The individuals were then divided into 3 classes: those that received a normal complement of sperm; those that received largely apyrene sperm; and those that mated but received no sperm. These results were then compared with the ovipositional response of virgin females - the average number of eggs per oviposition (Table 5).

Females which received a normal sperm complement or largely apyrene sperm oviposited at the same rate. Mated females which received no sperm had a higher oviposition response than virgin females. Caution must be taken in interpreting these data, because females classified as having received largely apyrene sperm may have used a great percentage of their complement of eupyrene sperm and may actually be no different from those that were recorded as having a normal ratio of eupyrene:apyrene sperm.

Also a female receiving a normal amount of sperm, even if largely apyrene, would more than likely receive an adequate amount of accessory secretion in the spermatophore. These data are therefore not conclusive as to whether sperm *per se* or accessory secretion elicits the ovipositional response. A search is underway to determine the effects on oviposition of various male accessory secretions. Four distinct accessory secretions can be found in the male cabbage looper reproductive tract. Through development of a method of artificial insemination, we hope that these secretions can be bioassayed for their ability to elicit a normal ovipositional response. Although it will be difficult to find, a chemical that would induce normal oviposition in a virgin female could be a future control mechanism.

The data presented in Table 5 indicate that females that received no sperm had a higher oviposition rate than virgin females. Therefore, it seems plausible that the oviposition response is caused by accessory secretion of the male incorporated into the spermatophore, rather than by the sperm *per se*. As shown by Holt and North (1970), the spermatophore bulb is filled early in the copulatory act with a clear fluid, and even females that receive no sperm from the spermatophore may receive small amounts of accessory fluid that could

TABLE 5.

The effect of type and quantity of sperm transferred on oviposition response of female cabbage loopers.

Type of sperm transferred	Number of individuals	Average eggs per oviposition
Normal eupyrene:apyrene	118	164.7
Largely apyrene	21	154.5
No sperm	50	57.6
Virgin females	28	31.4

TABLE 6.

The Inherited Sterility and Ovipositional Response of the F_1 Generation Produced by Mating an Irradiated Male and a Normal Female Corn Earworm

Dose to P_1 male	Percent egg hatch N female X P_1 male	N females X F_1 males		F_1 females X N males	
		Egg hatch	Avg. no. of eggs/female (% of control)	Egg hatch	Av. no. of eggs/female (% of control)
0	77.9	82.5	100.0	97.2	100.0
20	36.0	6.0	100.9	17.5	100.1

elicit normal oviposition. This is also borne out by examining the data of individual matings in this class of individuals. Although the average ovipositions are different, mated females that received no sperm either oviposited large numbers of eggs or oviposited no more than virgin females. This should be validated by determining if the spermatophore bulb was sufficiently filled with an accessory secretion at the time of mating.

Another important aspect of sperm transfer relates to the question of polygamy in Lepidoptera. Recently, J. Wendell Snow (personal communication), using single female traps in the field at Tifton, Ga., found that female corn earworms which had mated and received a normal complement of eupyrene and apyrene sperm attracted less males than did virgin females. This does not implicitly imply sperm *per se* as the important factor, but it re-emphasizes the importance of having released males that are capable of transferring normal amounts of sperm in future control programs. Field studies such as these are needed for the economically important lepidopterous species.

Basic Characteristics of Inherited Sterility in Lepidoptera

The phenomenon of progeny inheriting more sterility than their irradiated male parents is peculiar to species having holokinetic chromosomes. Therefore, the use of this phenomenon for economic control of insect populations is restricted to Lepidoptera and at least to some species of Homoptera and Hemiptera. In studies involving 10 lepidopterous species, the progeny from irradiated males were more sterile than were their male parents. The cabbage looper (North 1967, North and Holt 1968a, 1968b, 1970b), the sugarcane borer, *Diatraea saccharalis* (F.), (Walker and Quintana 1968), the tobacco budworm, *Heliothis virescens* (F.), (Proshold and Bartell 1970), the corn earworm, *Heliothis zea* (Boddie), (North and Holt, as presented later in this paper), the codling moth, *Laspeyresia pomonella* (L.), (Proverbs and Newton 1962), and the pink bollworm, *Pectinophora gossypiella* (Saunders) (W. Cheng and D.T. North, unpublished and A.C. Bartlett, unpublished) are examples of the delayed sterility that have already been found in economic species. Studies using the Hemipteran, the large milkweed bug, *Oncopeltus fasciatus* (Dallas), showed that sterility is inherited by the progeny of irradiated parents (LaChance *et al.* 1970, North, unpublished data), but the sterility in the F_1 generation is not as great as that exhibited by the parents. It is suspected that F_1 generation from irradiated males in Lepidoptera may be sterile because of chromosomal aberrations and deleterious effects on quantity and quality of the sperm since they definitely have complications in achieving successful sperm transfer. We have known for some time of the inability of F_1 male cabbage loopers to transfer sperm (North and Holt 1970b). This inability was also described by Proshold and Bartell (1970) in their work on the tobacco budworm.

The F_1 progeny in tobacco budworms from a cross involving an irradiated male and an unirradiated female have a longer developmental period than is considered normal and larval and pupal mortality are increased (Proshold and Bartell 1970). The authors also found a higher ratio of males to females. This sex distortion and the increased mortality in progeny from irradiated males were also observed in the codling moth by Proverbs and Newton (1962). Sex distortion is apparently a phenomenon that occurs in progeny from irradiated males in Lepidoptera. It has been observed in the codling moth (Proverbs 1962), the navel orangeworm, *Paramyelois transitella* (Walker), by Husseiny and Madsen (1964), the cabbage looper (North and Holt 1969), the tobacco budworm (Proshold and Bartell 1970), the corn earworm (North and Holt, as presented later in this paper), and the pink bollworm (W. Cheng and D.T. North, unpublished). The reasons for sex distortion are not known at this time. Experiments involving crosses with both male and female cabbage loopers (F_1's through F_5's) and showing sex distortion have shed very little light on the subject. Since in Lepidoptera the female is the heterogametic sex (see Mittwoch 1967 for references), sex distortion may well be caused by the expression of lethals induced on the X-chromosome; the resulting female progeny therefore succumb, and this results in a sex ratio in favor of the male. This sex ratio distortion is important in control and will be discussed later in this paper.

TABLE 7.

The Sterility Inherited by Cabbage Looper Progeny from an Irradiated Female Mated to an Unirradiated Male.

Dose to P_1 ♀♀ (krad)	I P_1 ♀♀ X N ♂♂		I F_1 ♂♂ X N ♀♀		I F_1 ♀♀ X N ♂♂	
	No. eggs	Percent hatch	No. eggs	Percent hatch	No. eggs	Percent hatch
0	10,352	85.9	4,463	96.6	2,538	90.7
10	9,531	38.2	3,171	81.2	2,914	72.8
15	7,882	14.7	1,480	65.7	3,186	82.8
20	5,108	6.6	2,017	41.3	1,006	83.4

TABLE 8.

The Theoretical Suppression Based on Laboratory Data of a Population of Lepidoptera Over Two Generations by a Single Release of Partially Sterile Males and/or Males and Females at a 9:1 Ratio.

Generation	Uncontrolled population a/	15 krad ♂♂ only	% Control	20 krad ♂♂ only	% Control	15 krad ♂♂ and ♀♀	% Control	20 krad ♂♂ and ♀♀	% Control
Initial	5,000	5,000	—	5,000	—	5,000	—	5,000	—
1	25,000	11,100	55.6	19,500	22.0	22,000	12.0	24,000	4.0
2	125,000	9,030	92.8	42,900	65.7	57,200	54.2	72,000	42.4

a/ Uncontrolled population assumed to increase at 5X rate for the several generations and the percent control achieved in the other populations was based on this figure.

Female progeny from a cross involving an unirradiated female and an irradiated male have greater fertility than do their male sibs. For example, when the male parent cabbage looper received 15 krad, the progeny of F_1 males times normal females had an egg hatch of 2.3%, whereas the progeny of F_1 females had an egg hatch of 19.5% (North and Holt 1968b). Egg hatch can be somewhat misleading in predicting the effect semisterile individuals will have on population suppression. F_1 females from an irradiated male parent will oviposit only half as many eggs as will normal females; therefore even though they have 20% fertility, their reproductive capacity is reduced 90%. Therefore, we feel that all considerations in assessing the value of releasing sterile and partially sterile moths should be based on the number of larvae produced per female. The fact that F_1 females from irradiated male parents oviposited fewer eggs was also substantiated for the tobacco budworm by Proshold and Bartell (1970).

The success of using delayed sterility in population suppression depends on a large percentage of the progeny coming from irradiated males (North and Holt 1969). It appears that the corn earworm is an ideal candidate for this type of release program (Table 6). The little effect irradiation has on the mating ability and sperm transfer of corn earworm P_1 and F_1 progeny suggests that fully sterile and partially sterile moths are capable of population suppression. A program where both partially sterile and fully sterile moths are released at different times could increase the efficiency of population suppression.

Irradiated Female Moths as a Source of Inherited Sterility

All of the basic studies and theoretical considerations for the use of inherited sterility for population suppression in Lepidoptera have been done on the basis of releasing only males. Because of the high cost of rearing and handling Lepidoptera, a more economical procedure might be the release of both sexes. There are two approaches to this method: (1) a dose where the inherited sterility in the irradiated female is equal to that of the male; or (2) treatments that render the female but not the male fully sterile.

To test these hypotheses, 3-day-old adult cabbage loopers were administered doses of 0, 10, 15, and 20 krad of gamma radiation and mated to unirradiated moths. The F_1 progeny from these crosses were then mated to unirradiated moths of the opposite sex, and fertility of the cross was determined. When adult male cabbage loopers are irradiated, the F_1 progeny are always more sterile than the P_1 parent, and the F_1 progeny from irradiated adult females are partially sterile but are not as sterile as the irradiated female parent (Table 7). Although progeny from irradiated female cabbage loopers are not as sterile as progeny from irradiated males, the male progeny are still the more sterile of the two sexes. It is obvious from these data that a dose cannot be used where the sterility of the progeny of the irradiated female is equal to that of the male. Though the female cabbage looper is sterilized at a lower dose (20-25 krad) than the male, the progeny from parents receiving this dose would be, from all that is presently known, quite noncompetitive. This would apparently preclude the possibility of irradiating and releasing both sexes.

Increased benefits would be incurred if both sexes could be released. Therefore, studies were conducted in laboratory population cages to determine the comparative values of releasing (1) only partially sterile males and (2) irradiated males and females. Table 1 shows that though the percentage is high, the number of eggs oviposited per female (at 20 krad) is half of that of the control. Therefore, the number of progeny actually being placed into the population by the irradiated female possibly would not be sufficient to have a deleterious effect on suppression.

North and Holt (1970b) showed the results of releasing into laboratory population cages, at a 9:1 ratio, both males and females that received 15 or 20 krad. Since it is felt that egg hatch alone in competition cages is not an accurate measure of the population suppression capacity of the treated insects, the number of larvae per female per day was used as the basis to calculate the reproductive potential in percent of control. In the first generation following release, suppression from the release of only males that had received 15 krad was equal to that obtained by the release of males and females that had received 15

and 20 krad. However, in the assessment of the F_2 populations, the reduction gained by the release of only males that had received 15 krad was far superior to that of any other group.

Table 8 shows a projected estimate of population suppression based on the release of partially sterile males and/or males and females. The basis for the calculations was that males and females were released in a 9:1 ratio into a natural population of 5,000 moths and that the normal reproductive rate of the uncontrolled population was five-fold for each generation (Knipling 1970). It appears that after a single release of males that received 15 krad, the population is suppressed for two generations and this is by far the most efficient method of suppressing a lepidopterous population. It should be remembered, however, that in small laboratory population cages all males are given a nearly equal chance to mate. Under natural field conditions, this most likely represents a gross overestimate of the capabilities of partially sterile males to suppress the population. On the other hand, in a small population cage, the fact that the males are in close proximity to the females could well mean that the advantage could be to the normal male; whereas in nature where there are not as many matings, the sterile or partially sterile male would have more impact. Recent test using field cage populations of cabbage loopers (Toba *et al.* 1970) showed that with one release of males receiving 15 krads, 92% control was achieved over two generations. The two experiments with two replications each in the field cages at Riverside are most encouraging because they indicate that the data obtained in population cages in a laboratory are valid.

Laboratory Population Suppression by the Release of Irradiated Inseminated Females and Males

With production techniques now available it is simple and cheaper to irradiate and release both sexes. Studies show that females inseminated before irradiation are sterile after they receive a dose of 15 krads (North and Holt 1970b). These tests involved laboratory populations of 10 pairs into which irradiated, inseminated females and irradiated males were released at a 9:1 ratio.

The results of these studies are given in Table 9. Only cages where there were no deaths of the natural population for a 5-day period are represented in these data. The released moths were marked with an artist's acrylic paint. By counting only population cages where there was no mortality of normal moths within the 5-day test period, the results are weighted toward the unirradiated moths. We feel this weighting in laboratory populations gives a more valid assessment in planning field cage tests. Table 4 shows that by releasing inseminated females and males irradiated with 15 krad, the first generation following release had an average hatch in 11 population cages of only 9%. This is in contrast to the fertility (88.5%) of the 4 control population cages.

The larvae were seeded on Ignoffo's medium (1963) in 260-ml. containers (20 larvae/container). The resulting pupae were sexed, and when all moths emerged, selections were made at random and the population cages were set up 10 pairs/cage. The second part of Table 4 shows that the fertility of the F_1 adult was higher than that of irradiated released moths (53.5%). However, the magnitude of the reductions in both generations is great enough to realize over 90% control from a single release.

Not only does the release of irradiated inseminated females and irradiated males give impetus to the use of delayed sterility for population suppression but this method may also, upon further refinement, prove to be ideal for releasing both sexes which have received a substerile dose. This could result in better suppression than when sterile insects are released. This technique would involve setting up large colony cages, allowing the moths to mate, collecting the eggs for one night, and then irradiating the moths and releasing them. A continuous progression of cages would be in use; thus there would be no need for separate colony cages, and the ease and cost of rearing would also be reduced. This continuous line of production would be an efficient method for a program of mass release in the field.

TABLE 9.

Suppression of Laboratory Populations of Cabbage Loopers by a Single Release or Irradiated (15 krad) Inseminated Females and Males at a 9:1 Ratio.

Population	Number of eggs	Number of replications	% Hatch
	1st Generation After Release		
Control	14,638	4	88.5
Population where irradiated inseminated ♀♀ and irradiated ♂♂ were released	19,477	11	9.0
	2nd Generation After Release		
Control	9,399	5	91.9
Population resulting from release of irradiated ♂♂ and inseminated ♀♀	30,048	10	53.5

TABLE 10.

Sterility Inherited by the Progeny of Male Cabbage Looper Pupae Exposed to 0.43 MeV Fast Neutrons. a/

Dose to P_1 generation	% hatch in % control (F_1 larvae)	% Hatch in % control (F_2 larvae)	
		♂♂	♀♀
0 (Control)	100.0	100.0	100.0
1 krad	97.9	92.2	100.0
3 krad	92.6	44.1	69.3
5 krad	89.1	39.4	—
10 krad	56.9	0.0	1.7
15 krad	15.3		
20 krad	12.9		

a/ Pupae were irradiated 72 hours before eclosion.

The Induction of Delayed Sterility in the Cabbage Looper by Fast Neutron Irradiation of Pupae

If the basic causes for delayed sterility in Lepidoptera are gross chromosomal rearrangements, it would be logical to assume that radiation of a high LET would be the most effective per unit of absorbed energy for induction. On this premise, male cabbage looper pupae (72 hr before emergence) were irradiated with various doses of fast neutrons (0.43 MeV), and the amount of sterility in the first and second generations was measured. Irradiations were conducted through the courtesy of the Brookhaven National Laboratory, Upton, Long Island, New York. The control group was shipped and handled in the same manner as the irradiated group. The pupae left our laboratory in the morning by air freight and arrived in Brookhaven that afternoon. They were irradiated the following morning and were back in our laboratory that evening. The results from these tests are presented briefly in Table 10. Since the previous studies using gamma irradiation to produce delayed sterility in the cabbage looper were done with adults, a comparison between the two irradiations of different LET cannot be made at this time.

It is interesting, however, to note that with fast neutron irradiation, the relationship between the amount of sterility induced in the P_1 generation and the F_1 generation was not entirely the same as was found for adults irradiated with gamma radiation. The male F_1's were more sterile than the female F_1's when their male parents were given the same dose. The doses, however, at which the offspring of fast-neutron-irradiated pupae became completely sterile were lower than those of gamma irradiation used to sterilize adults. In the previous studies with adults, 15-krad of gamma radiation was considered the minium dose to achieve full sterility. As can be seen in Table 10, 10 krad of N_f gave essentially complete sterility when pupae of this age were irradiated.

One characteristic that was different between the delayed sterility pattern achieved when pupae were irradiated with fast neutrons and when adults are given gamma rays was the fertility of the irradiated individuals and their F_1 progeny. When pupae were irradiated with neutrons (0-10 krad) their hatch was higher than that achieved when gamma radiation was used, and there was more sterility in the F_1 progeny. This could be a benefit in a release program since the higher fertility in the original irradiated parent would mean that a larger number of F_1's from the irradiated parent could be placed into a population. This would mean that the population suppression in the first generation would not be as great but should be increased in the second generation.

CONCLUSIONS

The ability of partially sterilized males to suppress a population in which they have been released has been successfully demonstrated in both laboratory and field-cage populations. In both of these types of test populations, a release of 9 irradiated to 1 unirradiated moth was sufficient to give 92% control over two generations. With the high cost of rearing and handling lepidopterous species, the ability to suppress populations to this degree with only a single release is advantageous. The use of delayed sterility in regions where there is migration from an overwintering population could well protect the outlying areas from ever being infested. This concept is discussed in detail by Knipling (1970).

The preliminary results from releasing irradiated inseminated females and males are most encouraging. The possibility of being able to release moths after they have mated and have been allowed to oviposit at least once (so that there is no need for the maintenance of separate colonies) in a mass rearing program has many economic advantages. The further refinement of the irradiation of an inseminated female could well lead to more efficient means of controlling Lepidoptera.

The use of neutrons as a source of radiation to induce delayed sterility is most encouraging, particulary because greater sterility is obtained in the F_1 generation than in the irradiated generation. The single most important factor in obtaining population suppression through the use of delayed sterility is the percentage of individuals obtained in

the F_1 generation that are from an irradiated parent. From previous calculations (North and Holt 1969) to get an effect of economic advantage, at least 60% of the F_1 population needs to come from the irradiated parent.

We believe the concept of releasing partially sterile moths for population control on a large scale is possible. Releasing irradiated inseminated females with partially sterile males can alleviate the necessity for sexing.

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IONIZING RADIATION AND VECTORS OF CHAGAS' DISEASE

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ABSTRACT

This paper reports on the application of ionizing radiation in a project related to the control of Chagas' disease in Venezuela. This disease, caused by the protozoan *Trypanosoma cruzi*, constitutes a major health problem throughout most of South America. In Venezuela, *Rhodnius prolixus* is one of the important vectors of the disease, and the approach to the problem has involved both studies on the feasibility of the sterile male technique and work on the field ecology of the insect, using radioactive tracers.

In *Rhodnius*, complete sterility is achieved only by radiation doses of more than 10 kR., a level of exposure which seriously interferes with behaviour. Thus, these insects were unable to compete with normal males. Further tests with males exposed to only 5 kR. showed, however, that although only 75% sterility was achieved at this dose, the males were much more active than untreated males, and mortality among progeny from normal females mated with the irradiated males was significantly higher than in normal nymphs. Males irradiated at 5 kR. were tested at varying ratios to normal males in established laboratory populations, and in all cases an initial density reduction was followed by a recovery in numbers, even in populations where all normal males had been replaced by treated individuals. Thus the use of sterile, or partially sterile, males for *R. prolixus* control did not prove feasible.

Ionizing radiation was also utilized in ecological studies with *R. prolixus* and *Triatoma maculata*. Field tests with adults of these two species were designed to evaluate dispersal, resting-place preferences and survival. Various tagging procedures were tested, and it was found that a practical method consisted of injecting radioactive platinum-iridium (Ir^{192}) wires into the abdomens of the insects. The results of field experiments indicate that dispersal was mainly motivated by starvation. Preferred habitats are certain species of trees and thatched houses. The average survival expectancy related to predation pressure, migration rate, and dispersal limits the probability of house infestation by wild specimens.

INTRODUCTION

Chagas' disease, although basically a neotropical public health hazard, is distributed from 42°N to 45°S throughout the Americas. The disease is caused by *Trypanosoma cruzi* a protozoan affecting mainly the heart by its invasion of the myocardium. Vectors are triatomid bugs and the most important reservoirs are mammals. Transmission is by direct contact with faeces from infected vectors, and to a lesser extent by contaminated food, blood transfusion and congenital infection.

It is estimated that in the Americas about 30 million people are infected by *T. cruzi* and of those, eight million already suffer heart and other Chagas' disease damage.

Variances in vector adaptation and behaviour are large, ranging from cold to tropical climates and from outdoor to indoor habits. Although most species inhabit certain types of vegetation, vertebrate nests, and landscapes, the vectors of main public health importance are those adapted to human dwellings. House infestation density is closely related to house-type insects, and the thatched mud-walled hut, so common in the tropics, provides the most suitable indoor habitat for Chagas' disease vectors.

Triatomid control is presently accomplished by means of housing improvement and insecticides. Both measures are expensive and insecticides have the added drawback of high toxicity.

Ionizing radiation in relation to the study of the vectors has been used in two ways; one, to induce sterility, and the other as a tagging agent for ecological studies. This paper reviews results obtained from tests done in Canada and Venezuela with *R. prolixus* and *T. maculata,* two important vectors of Chagas' disease. Details of the material and methods can be found in the publications given as references.

I. STERILITY STUDIES

Initial investigations to determine the feasibility of applying the sterile male technique suggested that *R. prolixus,* an important indoor vector, could be a suitable subject. No great difficulties were encountered in its mass rearing (1), and the release of sterile individuals in the peridomestic environment, in conjunction with indoor spraying of non-persistent insecticides, offered a possible means of arresting house infestation. Direct release of sterile individuals within houses was not contemplated since both sexes of *R. prolixus* are disease vectors throughout nymphal and adult stages.

Sterility was induced either by X-rays or by gamma radiation and the results from both were similar. Batches of 20-50 specimens were exposed and the parameters studied were changes in fertility, oviposition in normal females mated to treated males, movement, longevity, mating frequency and competitiveness. The effect of time and sequence between feeding and irradiation were observed. Also, some physiological and cellular alterations were noted.

Results

Both Venezuelan (2),(3) and Canadian (4) studies agreed in that the adult male was the most suitable stage for irradiation. Eggs exposed to as low as 100 R. produced few nymphs and gave variable effects in the small number that did reach adulthood. Nymphs exposed to radiation tended to produce a large proportion of nonfunctional adults. Adult females when exposed to the same doses as males were less sterile but more functionally damaged than the males. Complete male sterility was achieved only by exposures to more than 10 kR., but this radiation level also caused damage which inhibited mating capability. However, it was noted that the reproductive potential of males exposed to only 5 kR. was altered sufficiently to warrant an investigation of their effects when introduced into normal populations. These alterations consisted of a 75% reduction in fertility, a 14% increase in movement, a 50% increase in mating frequency, and a 29% increase in induced oviposition among females mated to them. This last phenomenon in *R. prolixus* is a function of mating frequency and its increase was probably due to a general physiological stimulus generated by exposure to less than 10 kR.;this stimulus was also reflected in the increased movement. All differences except movement and mortality were significant.

Mortality in descendants from males exposed to 5 kR. and normal females was more than twofold that which is normally expected. Exposure to less than 5 kR. produced little sterility and larger exposures inhibited mating capability. Time itself and mating frequency increased sterility since radiation affected mainly the spermatogonia and not the spermatozoa. Time and feeding increased mortality and general damage by accelerating cellular activity (5) which makes evident latent cell damage (6). Competitiveness in mating when these males were challenged by the presence of normal ones was found to be adequate.

These characteristics of males exposed to 5 kR. generated tests to observe the effect of partial sterility on laboratory populations of *R. prolixus* (7). Males were introduced in different proportion to normal males as found in laboratory populations. Some decline was noted only in populations where males were introduced at 4 to 1, or higher, ratios and in populations where all normal males were replaced monthly by treated males. However, even in this last extreme test,density recovered after the initial decline. Detailed studies made to

determine the probable causes for this recovery revealed that the detrimental effects in descendants disappeared after the F_3 generation and that individual variances in radiation resistance, or, shortcomings in the irradiation method probably allowed some males in each treated batch to remain unaffected. This last test indicated that the use of radiation induced sterility as a means for *R. prolixus* control was not feasible.

II. ECOLOGICAL STUDIES WITH TAGGED INDIVIDUALS

Until 1960 the information on Chagas' disease vectors was based on laboratory reared specimens and superficial field observations. It was taken for granted that vectors depended mainly on human and bird transportation for their dispersal, that field longevity approached one year and that distribution of specimens in indoor structures was uniform with no dense aggregations of insects.

Ecological studies, using radioisotope tagged adult specimens were made to test these assumptions.

A tag with an activity of 75 mc. was found to be adequate for detection up to a distance of 7 m. with Geiger and scintillation counters.

The tag itself went through a series of modifications. At first Co^{60}, in nitric acid and acetone, was mixed with cellulose acetate and a droplet placed on the thorax of laboratory bred *R. prolixus.* (2). These tags did not adhere to the insects and data from subsequent field tests were incomplete due to tag losses. Nevertheless it was observed in these tests that *R. prolixus* had a small home range, preferring to remain near its food sources, and that at least one specimen left and returned to the house where it was released. Other tests using Co^{60} wires, 1 mm long by 0.12 mm diameter, fixed with epoxy to the thorax, demonstrated that adults of *R. prolixus* could move by their own locomotion from palm tree to palm tree and from the trees to houses, and also from house to house if distances were short (8). Movement apparently was restricted to crawling as no flying activity was indicated. A useful observation from these tests was the unsuitability of laboratory bred specimens since they moved in rhythm to the 14 day feeding cycle used in the insectary. Since tags continued to be dropped, W.F. Baldwin of the Atomic Energy of Canada Ltd., Chalk River, Ontario, tested the same Co^{60} wires inserted in the connexivum but results were negative due to Co toxicity for *R. prolixus.* A solution to the tag loss and toxicity was found by covering the wires with gold and inserting them in the connexivum (9).

Although tests using this method were suitable, it was noted that occasionally domestic fowl pulverized the wire when ingesting tagged *R. prolixus.* Finally the use of platinum-iridium (Ir^{192}) wire inserted in the abdomen of field collected specimens eliminated these problems (10,11). Inasmuch as the effect of radiation on tagged specimens was not detectable during the initial 40 days, only data collected during that period were included in the results.

To minimize possible disturbances caused by handling and tagging, both *R. prolixus* and *Triatoma maculata* were released during the daytime when their activity was at the lowest ebb. Release was made in different types of outdoor habitats, houses and at various distances between habitats.

Visits were daily during the first week and weekly thereafter. During each visit resting places were noted and all insects found dead, or assumed dead by lack of movement, were removed. Predators were determined by examining their feces for wires or by the presence of mutilated tagged specimens in their shelter. To avoid excessive fields of radiation and effects of crowding no more than seven tagged individuals were released at each habitat.

Results

Table I gives a general tabulation of results. Although emigration occurred during the 40 days of the test some specimens remained at the release place throughout that time. Of those released in vegetation, *T. maculata* shows a greater tendency towards movement. The differences between the ones released in vegetation and those released in houses suggest

TABLE I

Results of tagging experiments involving *Rhodnius prolixus* and *Triatoma maculata* in VENEZUELA

Results	Released in vegetation		Released in houses	
	R.p.	T. m.	R. p.	T. m.
Total number of specimens	54	90	46	26
% Remaining at release place	12.9	2.4	58.6	61.6
% Leaving release place	87.1	97.6	41.4	38.4
% Reaching houses	27.8	8.2	8.7	0.0
% Reaching vegetation	12.9	17.7	0.0	0.0
% Not reaching other places	46.4	71.7	32.7	38.4
% Leaving release point during initial 5 days	63.0	64.5	41.4	53.9
Mean dispersal distance (m.)	3.1	3.2	2.2	3.2
Maximum dispersal distance (m.)	15.0	15.0	4.0	7.6
Average survival in days	22.6	18.0	19.1	17.9
% Alive at the end of test	9.2	2.4	19.6	11.5
% Caught by predators	83.4	71.8	63.0	73.2
% by arthropods	7.4	34.2	6.5	50.0
% by fowl	66.7	32.9	47.8	15.5
% by other vertebrates	9.3	4.7	8.7	7.7
% Dead without predation signs	0.0	3.5	13.1	11.5
% Missing	7.4	22.3	4.3	3.8

that, due to a continuous food supply and adequate resting places, houses offer a more stable habitat than vegetation. The dispersal trend indicates greater movement from vegetation to house in *R. prolixus* and from vegetation to vegetation in *T. maculata.* No movement from house to vegetation was noted in either species. Predator activity was greater outdoors than indoors. Since field collected insects included specimens at all degrees of starvation, movement began at the moment of release. The increased dispersion noted during the first five days suggests either the presence of some starved specimens or, most likely, that the release point was not the one most suitable for the insect. That specimens released indoors tend to migrate less than others suggests that in houses adequate resting places are closely situated. Dispersal was quite similar in both species, but the differences between the two habitats again indicates the greater environmental stability found in houses.

Average survival was similar in all four variants and much lower than it was previously assumed. The percentage still alive at the end of the test again favors the indoor types and *R. prolixus.* Although general predation pressure is not excessively dissimilar, the predators involved indicate that *T. maculata* is mainly affected by other arthropods while *R. prolixus* is affected mainly by fowl. This offers a possible explanation why *T. maculata* is likely to invade houses freed from arthropods after insecticide spraying operations. If this is so then the replacement of *R. prolixus* by *T. maculata* as the main indoor vector, now occurring in some parts of Venezuela, could be assumed to be a man induced phenomenon. The greater amount of dead specimens, with no predation signs, found in houses is probably due to unreported use of domestic insecticides and not to a direct action by the inhabitants since no killing of vectors was reported. Release areas were visited for two months after the end of the tests in search of the missing specimens. The percent reported missing could be assumed to have been ingested by flying predators and the high proportion of missing *T. maculata* in the outdoors suggests a predator preference for the species in that environment.

Detailed observations indicated that when outdoors, *R. prolixus* prefers palm trees, bird nests and, apparently, no other outdoor habitats.

In the houses, 44% of *R. prolixus* found shelter in thatched roofs, 31% in household articles and 25% in walls. *T. maculata* showed similar behaviour but outdoors it found shelter in fowl pens and any vegetation with rough bark. In all cases, the vectors tended to remain close to beds and other sleeping places and none were found in corrugated metal roofs. This dependence of shelter occupancy on its distance from food, even when suitable resting places were plentiful throughout the environment, suggests that the relationship of shelter - distance - food could be considered as the main component of the factors that limit Chagas' disease vector populations. These results only partially indicate the magnitude of the public health problem created by the proximity of infested outdoor habitats to houses. The rate of emigration from the outdoors towards the house, not by any preference, but most probably due to population pressure and random movement, must be sufficient to overcome the probability of the death of the insect while enroute to, and while becoming established in, the house; from the data the probabilities can be calculated and the infestation rates of different species under different conditions can be evaluated. Regarding vector control, insecticide application costs could be reduced considerably by applying them selectively instead of over all indoor areas; this would also avoid the elimination of arthropod predators that apparently keep *T. maculata* out of houses. As supplementary measures replacement of thatched roofs by laminated roofing material and clearing of certain vegetation types in the immediate surroundings of rural houses should be encouraged.

In conclusion, the use of ionizing radiation in relation to Chagas' disease vector control has contributed to the increase of the knowledge about them even though it failed to provide an adequate means for their control. The success with radioisotope tagged specimens in ecological studies has made their inclusion a necessity in the evaluation of control operations and in the development of density evaluation methods.

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ACARINE FAUNA IN SOUTHEASTERN MANITOBA: I – FOREST SOILS

by E.T. Oswald and L.W. Minty

INTRODUCTION

The acarine fauna of various soil and vegetation cover types have been reported from Europe (Drift, 1951; Evans, 1951; Macfadyen, 1952; Murphy, 1953; Evans, Sheals and Macfarlane, 1961; Hayes, 1965; Madge, 1965; Marcuzzi, 1965; Greenslade and Greenslade 1967) and North America (Hammer, 1952, 1955; Hirston and Byers, 1954; Wallwork, 1959; Woolley, 1960; Marshall and Kevan, 1964; Dowdy, 1965; Marshall, 1968). The reports in North America are from widely scattered localities and often the faunas are based on a few random collections rather than a systematic collecting method. Consequently it is difficult to make quantitative comparisons of the faunas and their seasonal fluctuations. Since the emphasis in biological science at present is on the ecosystem, it is desirable to know what species occur in each ecosystem and how the populations fluctuate under different conditions.

The present preliminary study is a comparison of the acarine fauna of 12 forest sites in Manitoba, Canada (Fig. 1). Some of the sites differ only in vegetation cover while others differ in soil type and moisture relations. Most of the collections have been identified at least to genus either by V.G. Marshall, Department of Fisheries and Forestry, Forestry Service, Chalk River, Ontario or by E.E. Lindquist, Department of Agriculture, Entomology Research Institute, Ottawa, Ontario.

MATERIALS AND METHODS

One core sample from each of the 12 sites (Table I) was taken every 4 weeks from 1 April 1968 to 6 January 1969. Heavy snow cover (approximately 45 cm) prevented sampling between February and April. A volumetric soil sampler designed by Vannier and Vidal (1965), modified by V.G. Marshall (personal communication) and built by Kraftsman Machine Co. Ltd., Winnipeg Manitoba with an area of 22 cm^2 and a volume of 330 cm^3 was employed. The core tube of the sampler was 15 cm long but cut transversally so that each core could be divided into two samples each 7.5 cm long. The temperature of each sample was recorded prior to sampling by placing a glass thermometer at depths of approximately 3 cm and 10 cm adjacent to the sampling sites. Each core tube with its sample was inverted into a Berlese funnel for extraction. A battery of 60-watt light bulbs was used to extract stages of mites from samples into vials. Seven days were allowed to dry the soil and complete the extraction. On every third collecting date the samples were extracted into 70% alcohol and the others into a saturated picric acid solution. Although alcohol is not as efficient for extraction purposes as picric acid, it does not discolor the mites and thus obscure some of the taxonomic characters. Mites submitted to specialists for identification were mounted on slides in Hoyer's medium (Baker and Wharton, 1952).

RESULTS

Seventy species of mites were identified consisting of 58.6% cryptostigmatids, 27.1% mesostigmatids, 12.9% prostigmatids and 1.4% astigmatids. Some additional forms, mostly larvae, could not be identified and are omitted from this report. In numbers of individuals the cryptostigmatids comprised 86% of the extracted fauna, the mesostigmatids 9%, the astigmatids 3%, and the prostigmatids 2%.

An annotated list of the species obtained in this study is presented in Table II. The sites from which each species was found and the site with the highest annual average of the species are indicted. Mites usually attain their highest densities in the surface layer but

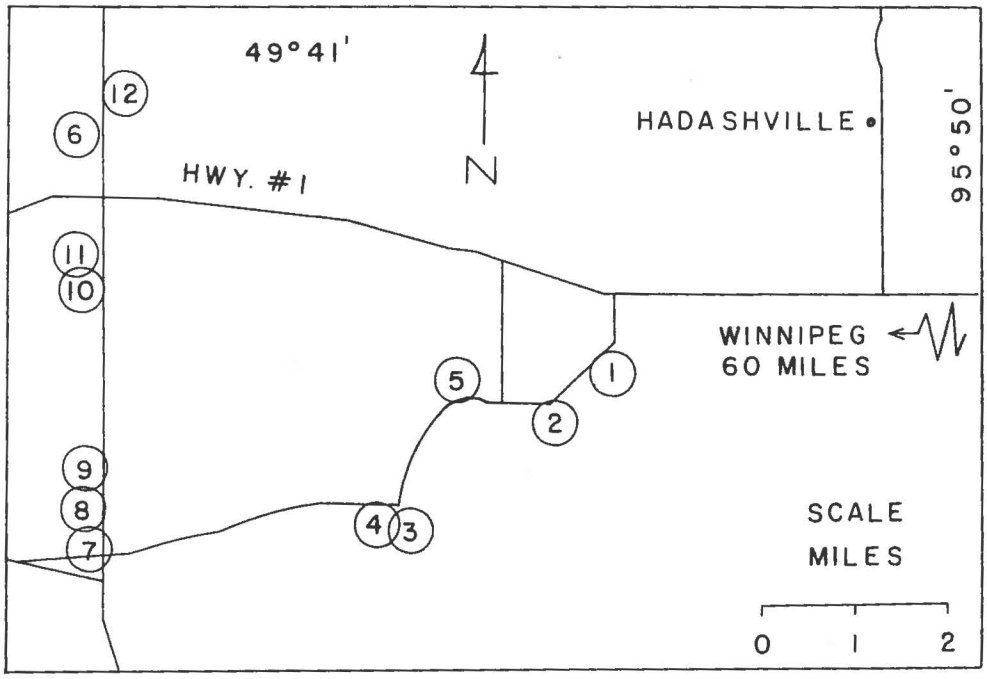

Figure 1. Map of study area showing the sites from which collections were made.

TABLE I

Description of Sampling Sites

Site No.	Moisture class *	Dominant vegetation	Subordinate vegetation type	Depth of organic matter	Soil type
1	dry	Jack Pine	discontinuous moss-lichen	2-4 cm	sand
2	dry	Jack Pine	continuous feathermoss	2-4 cm	sand
3	dry	Jack Pine	continuous feathermoss	2-4 cm	sand
4**	dry	ericaceous shrubs	continuous forbs	2-4 cm	sand
5	moist	White Spruce	discontinuous forb-moss	6-9 cm	loamy sand
6	moist	Aspen	continuous shrub-forb	5-7 cm	loamy sand
7	wet	Black Spruce	Sphagnum	50 cm	organic
8	wet	Black Spruce	Sphagnum	58 cm	organic
9	wet	Black Spruce	shrub-sphagnum	45 cm	organic
10	wet	Larch	Sphagnum-feathermoss	275 cm	organic
11	wet	Black Spruce	forb-moss	60 cm	organic
12	wet	Black Spruce	Sphagnum	45 cm	organic

* Dry- no free water in solum except for brief periods after rains and during snow melt; water table at about 120 cm in spring and 240 cm in autumn.

Moist- free water within 30 cm of surface for significant periods but not all of snow-free period; water table at about 25 cm in spring and 70 cm in autumn.

Wet- free water within 30 cm of surface for nearly all the snow free period; water table at about 5 cm in spring and 30 cm in autumn.

**This was a typical jack pine site but was clear-cut approximately ten years ago and there is essentially no arboreal regeneration.

Table II. Annotated List of Acarina: A - Sites, B - Site most Abundant and Annual Population Average, C - Layer, D - Population Peak. (See text for further explanation)

ASTIGMATA

Acaridae

Rhizoglyphus sp.
A. all
B. 3 (22,850/m^2)
C. surface & subsurface
D. December

PROSTIGMATA

Cunaxidae

Cunaxa setirostris Hermann
A. all except No. 6
B. 2 (620/m^2)
C. mostly surface
D. July & January

Rhagidiidae

Rhagidia sp.
A. all except Nos. 1 & 4
B. 6 (830/m^2)
C. mostly surface
D. none

Scutacaridae

Scutacarus sp.
Rare

Stigmaeidae

Ledermuelleria rhodomela Koch
A. 1, 3, 4, 6, 7, 9, 11, 12
B. 9 (540/m^2)
C. all surface
D. January

Ledermuelleria segnis Koch
A. 1, 2, 3, 7, 8, 9, 10, 11
B. 2 (500/m^2)
C. all surface
D. none

Stigmaeus scaber Summers and *S. sphagneti* Hull
A. all except No. 9
B. 3 (540/m)
C. all surface
D. none

Trombidiidae

Microtrombidium sp., near *parvum* Oudemans
A. all except Nos. 1 & 2
B. 5 (330/m^2)
C. mostly surface
D. May & November

Tydeidae

Lorryia sp.
A. 1, 2, 3, 4, 8, 9, 10, 11
B. 2 (200/m^2)
C. surface & subsurface
D. none

MESOSTIGMATA

Ascidae

Asca aphidioides L. and *A. garmani* Hurlbutt
A. all
B. 3 (2,110/m^2)
C. surface & subsurface
D. December

Cheiroseius sp.
A. 1, 6, 7, 8, 10, 11, 12
B. 8 (700/m^2)
C. mostly surface
D. none

Digamasellidae

Digamasellus angulosus Willmann
A. 5
B. 5 (860/m^2)
C. surface & subsurface
D. December

Digamasellus sp.
A. 1, 2, 4, 7
B. 4 (620/m^2)
C. surface & subsurface
D. January

Laelaptidae

Hypoaspis nolli Karg
A. all except No. 9
B. 8 (2,190/m)
C. surface & subsurface
D. none

Neoparasitidae

Ololaelaps sp., near *venetus* Berlese
A. 2, 3, 6, 9, 10, 11, 12
B. 10 (290/m^2)
C. mostly surface
D. none

Parholaspidae

Neparholaspis swartae Marshall
Rare

Phytoseiidae

Typhlodromus sp.
A. 1, 2, 3, 4, 5, 6, 7, 9
B. 2 (1,610/m^2)
C. mostly surface
D. none

Rhodacaridae

Gamasellus bellavistae Emberson and *G. vibrissatus* Emberson
A. all except No. 4
B. 5 (2,020/m^2)
C. mostly surface
D. April & December

Sejidae

Sejus americanus Banks
A. 5, 6, 7, 8, 10, 11
B. 5 (620/m^2)
C. mostly surface
D. none

Uropodidae

Dinychus sp.
A. 5, 6, 7, 8, 9, 11, 12
B. 5 (580/m^2)
C. surface & subsurface
D. none

Trachytes sp., near *pyriformis* Kramer
A. 6, 7, 8, 9, 11, 12
B. 12 (660/m^2)
C. mostly surface
D. none

Veigaiidae

Veigaia mitis Berlese
A. 1, 5, 7, 8, 9, 11, 12
B. 8 (820/m^2)
C. surface & subsurface
D. October

Zerconidae

Parazercon radiatus Berlese and *Parazercon* sp., near *sarekensis* Willmann
A. all except No. 10
B. 5 (3,720/m^2)
C. surface & subsurface
D. May & December

Zercon alaskensis Sellnick and *Zercon* sp., near *peltatus* Koch
A. all except No. 5
B. 2 (1,690/m^2)
C. mostly surface
D. October

CRYPTOSTIGMATA

Achipteriidae

Achipteria sp., near *nitens* Nicolet
A. all except No. 11
B. 5 (6,080/m^2)
C. mostly surface
D. none

Brachychthoniidae

Eobrachychthonius latior Berlese
Rare

Liochthonius sp.
A. 3, 4, 5, 7, 8, 9, 10, 11, 12
B. 8 (2,330/m^2)
C. mostly surface
D. April & December

Camasiidae

Camisia sp.
A. 1, 2, 4, 8, 9, 10
B. 1 (660/m^2)
C. surface only
D. May

Heminothrus thori Berlese
A. 1, 3, 7, 9, 10, 12
B. 10 (4,510/m^2)
C. mostly surface
D. November

Uronothrus sp., near *kochi* Willmann
Rare

Carabodidae

Carabodes sp. 1
A. 1, 2, 3, 4, 5, 10, 12
B. 2 (8,970/m^2)
C. surface only
D. December & January

Carabodes sp. 2
A. all except Nos. 7 & 10
B. 1 (660/m^2)
C. surface only
D. June

Cepheidae

Cepheus sp., near *corae* Jacot
A. 3, 5, 6, 7, 9, 10, 12
B. 3 (290/m^2)
C. mostly surface
D. November & April

Ceratozetidae

Ceratozetes sp. 1
A. all
B. 12 (4,510/m^2)
C. surface & subsurface
D. none

Ceratozetes sp. 2
A. all
B. 8 (12,190/m^2)
C. surface & subsurface
D. April

Fuscozetes bidentatus Banks and *F. fuscipes* Koch
A. 2, 3, 4, 5, 6, 9, 12
B. 6 (4,830/m^2)
C. surface only
D. none

Propelops sp., near *pinicus* Jacot
A. 2, 4, 5, 6, 7, 8, 9, 10, 12
B. 6 (750/m^2)
C. surface only
D. April

Cosmochthoniidae

Trichthonius majestus Marshall & Reeves
Rare

Damaeidae

Belba sp., near *tatrica* Kulczynski
Rare

Eniochthoniidae

Hypochthoniella minutissimus Berlese
A. all except No. 1
B. 5 (5,910/m^2)
C. mostly surface
D. April

Eremaeidae

Eremaeus sp.
Rare

Euphthiracaridae

Euphthiracarus sp.
Rare

Rhysotritia ardua Koch
A. all except Nos. 2 & 7
B. 10 (1,530/m^2)
C. surface & subsurface
D. April

Galumnidae

Pergalumna sp.
A. all
B. 2 (1,240/m^2)
C. mostly surface
D. April

Gustaviidae

Gustavia sp.
A. all except No. 4
B. 6 (1,290/m^2)
C. mostly surface
D. December

Gymnodamaeidae

Allodamaeus sp.
A. 4, 6, 7, 12
B. 4 (910/m^2)
C. surface only
D. January

Gymnodamaeus gildersleeveae Hammer
A. 1, 2, 4
B. 4 (1,940/m^2)
C. surface only
D. May & January

Haplozetidae

Peloribates sp.
A. all
B. 1 (10,870/m^2)
C. mostly surface
D. June & December

Hypochthoniidae

Hypochthonius rufulus Koch
A. 7, 8, 9, 10
B. 7 (2,890/m^2)
C. surface & subsurface
D. January

Malaconothridae

Malaconothrus sp.
A. 5, 8, 9, 10, 11, 12
B. 12 (2,210/m^2)
C. surface & subsurface
D. April & September

Mesoplophoridae

Archoplophora laevis Jacot
A. all except Nos. 1, 4, 10
B. 12 (14,170/m^2)
C. surface & subsurface
D. April & December

Metrioppiidae

Ceratoppia bipilis Hermann
A. 1, 2, 3, 7, 10, 11, 12
B. 12 (210/m^2)
C. surface only
D. none

Ceratoppia sp.
A. 2, 3, 4, 5, 7, 12
C. surface only
Scarce

Nanhermanniidae

Nanhermannia elegantula Banks
A. 5, 6, 7, 8, 9, 10, 11, 12
B. 10 (6,080/m^2)
C. surface & subsurface
D. December

Nothridae

Nothrus silvestris Nicolet
A. 3, 7, 8, 9, 10, 11, 12
B. 12 (3,470/m^2)
C. surface & subsurface
D. July & January

Oppiidae

Oppia minus Paoli and
Oppiella nova Oudemans
A. all
B. all (17,930-67,390/m^2)
C. surface & subsurface
D. none

Oribatulidae

Scheloribates sp., near
pallidulus Koch
A. all except Nos. 7, 10, 11
B. 3 (2,270/m^2)
C. mostly surface
D. April & December

Pelopidae

Eupelops sp.
A. 1, 2, 3, 4, 7, 9, 10, 11
B. 1 (6,030/m^2)
C. mostly surface
D. April & November

Phthiracaridae

Hoplophorella sp.
Rare

Phthiracarus sphaerulus Banks
A. all except No. 2
B. 5 (4,750/m^2)
C. surface & subsurface
D. April & December

Steganacarus diaphanum Jacot
Rare

Tectocepheidae

Tectocepheus velatus Michael
A. all
B. 2 (7,690/m^2)
C. mostly surface
D. none

Trhypochthoniidae

Trhypochthonius tectorum Berlese
A. all except Nos. 6, 11
B. 2 (2,900/m^2)
C. mostly surface
D. none

sometimes are nearly as abundant in the subsurface layer. Three categories are used in Table II; those found only in the surface layer, those with subsurface densities less than 50% of the surface layer, and those with subsurface densities 50% or greater of the surface layer. The time of annual population peaks are also indicted for each species. In some cases two very similar species could not be distinguished under a dissecting scope and were counted together.

The most common species, comprising 71% of the acarine fauna, were *Archoplophora laevis, Ceratozetes* spp., *Nanhermannia elegantula, Oppia minus, Oppiella nova, Parazercon* spp., *Peloribates* sp., *Phthiracarus sphaerulus, Rhizoglyphus* sp., and *Tectocepheus velatus.* These were all cryptostigmatids except *Parazercon* and *Rhizoglyphus.* Species represented by very few individuals included *Belba* sp., *Eobrachychthonius latior, Eremaeus* sp., *Euphthiracarus* sp., *Hoplophorella* sp., *Neparholaspis swartae, Scutacarus* sp.,*Steganacarus diaphanum, Trichthonius majestus* and *Uronothrus* sp.

There was no clearcut separation to habitat preference at the suborder level, however, a marked preference was often observed by some species. The species restricted to dry sites were *Gymnodamaeus gildersleeveae* and *Uronothrus* sp., and those relatively most abundant in dry sites were *Belba* sp., *Carabodes* spp., *Camisia* sp., *Digamasellus* sp., *Eupelops* sp., *Peloribates* sp., *Scheloribates* sp., *Trhypochthonius tectorum* and *Typhlodromus* sp. These latter species when found in wet sites most frequently occurred in the surface samples. The species restricted to wet sites were *Hypochthonius rufulus* and *Trichthonius majestus,* and those relatively most abundant there were *Archoplophora laevis, Ceratozetes* sp. 2, *Cheiroseius* sp., *Eobrachychthonius latior, Malaconothrus* sp., *Nanhermannia elegantula, Nothrus silvestrus, Achipteria* sp., *Sejus americanus, Trachytes* sp., and *Veigaia mitis. Digamasellus angulosus* was the only species confined to moist sites.

Generally the various acarine groups were more abundant in winter and spring and scarce in late summer and early autumn (Fig. 2). Similar trends in seasonal fluctuations among forest soil mites were also observed by Madge (1965) and Block (1966) in England. The temperatures of the samples generally attained a high of about 18°C in July and were frozen from mid November to early April (Fig. 2); the lowest temperature recorded was minus 9°C in January. From late April to mid-October the surface temperatures were consistently higher than the subsurface temperatures but the only appreciable difference occurred during late April. From November to April the surface temperatures were slightly lower than the subsurface temperatures.

DISCUSSION

Although most of the species found in this investigation have been reported from various parts of North America or Europe (Woolley, 1960; Marshall and Kevan, 1964; Madge, 1965; Marshall, 1968) some have not previously been reported from Canada and others may be new to science. *Archoplophora laevis, Digamasellus angulosus, Fuscozetes bidentatus, Ledermuelleria rhodomela* and *Sejus americanus* were among those not listed by Hammer (1952), Marshall and Kevan (1964) or Marshall (1968) as occurring in Canada; however most of their work was on the cryptostigmata and only two of these mites are in that suborder. *Trichthonius majestus* was recently described by Marshall and Reeves (1970). Several genera including *Cepheus, Euphthiracarus, Gustavia, Hoplophorella, Ledermuelleria,* and *Rhizoglyphus* contain undescribed species.

The number of mites per square meter varied seasonally and from site to site. The undisturbed dry sandy sites had a yearly average of 75,032 mites/m^2 in the top 15 cm with 78% of these being in the surface 7.5 cm. The highest average at one collecting period, combining surface and subsurface samples, was 152,577 mites/m^2. The wet sites had the highest yearly average, 79,593 mites/m^2 in the top 15 cm with 73% in the top 7.5 cm and a peak collection period of 145,480 mites/m^2. The cut over jack pine site had the smallest population with an annual average of 40,992 mites/m^2. The moist sites had a yearly average of 74,615 mites/m^2 and a peak collection average of 160,907 mites/m^2. It is difficult to compare these figures with studies conducted in other areas and sites because of the differences in techniques used by the researchers. Macfadyen (1955, 1961, 1962) and

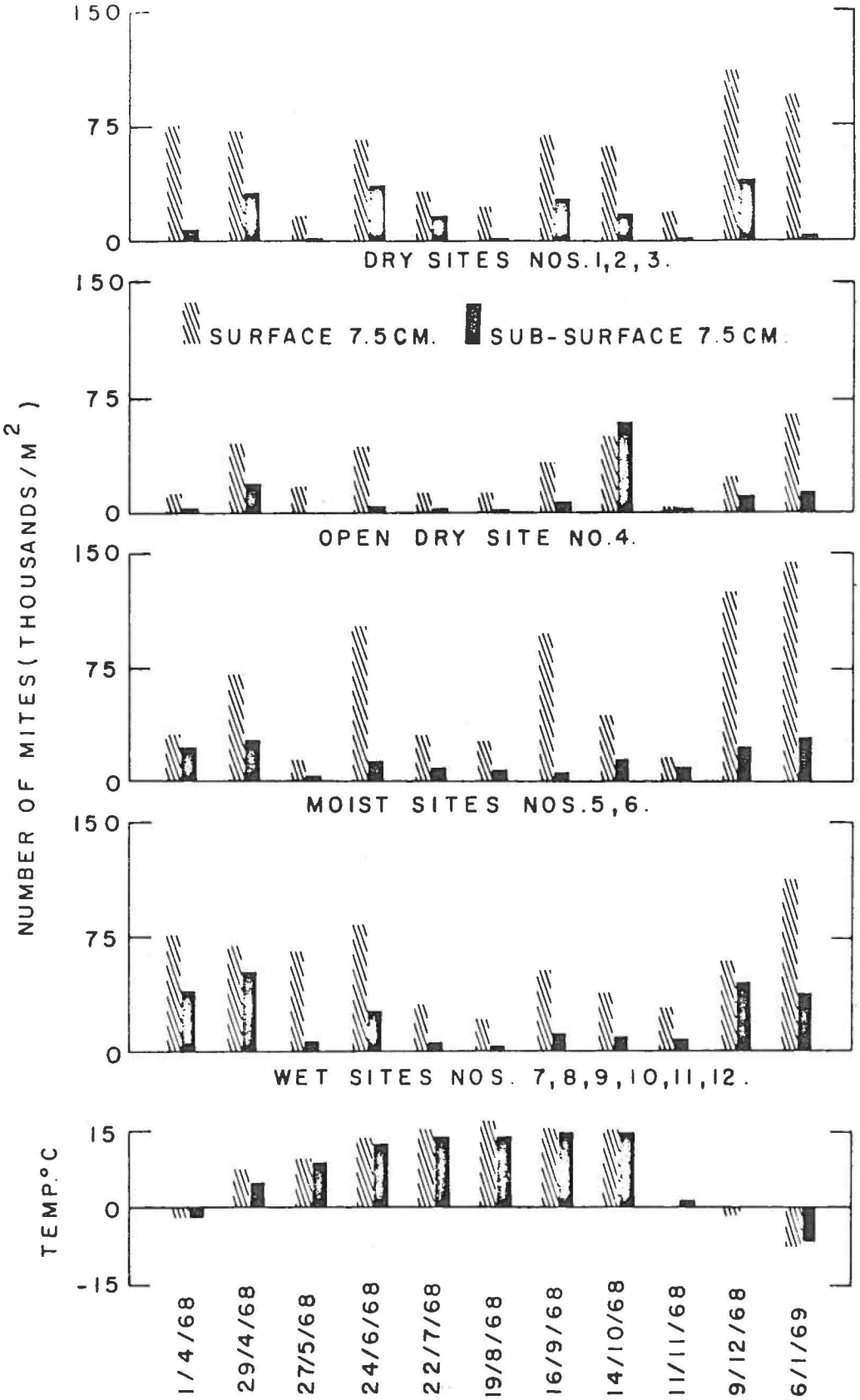

Figure 2. Average populations in surface and subsurface samples for each site type on 11 collecting dates and the average temperature of the samples.

Murphy (1962) have evaluated several extraction techniques and found the number of species and individuals to vary with the method but that different methods were better for different soil types. Other factors influencing the number of mites extracted include the depth, area, and phenological time of sampling, the disturbance of the sample, and the collecting medium employed. Hairston and Byers (1954) reviewed the number of mites obtained in several studies of various sites and indicated the lack of comparative estimations of population size among different studies. The reported number of mites in forest communities varies between 20,000/m^2 and 341,000/m^2 (Marshall and Kevan,1964;Dowdy, 1965; Madge, 1965; Block, 1966; Marcuzzi, 1966; Berg and Ryke, 1967; Greenslade and Greenslade, 1968). The degree of variance that can be ascribed to habitat difference in these studies can not be evaluated because the techniques employed in each case differ.

The ecology of soil mites is not well known but a few studies, mostly in the last few years, have been made on their importance to the soil community. One of the greatest hinderances appears to be the difficulty to rear single species from field populations in the laboratory so that life history and other biological studies can be conducted in detail. Often nymphal stages require a specific food material and perhaps environmental conditions that differ from the adult (Sengbusch, 1954; Hartenstein, 1962; Murphy and Jalil, 1964; and Rodriquez, 1964). Indications are that the feeding habits of soil mites vary considerably among species but much of the specific data has been obtained through inconclusive laboratory analysis. Fungi, algae, protozoa, insect larvae, and raw organic matter are among the materials that soil mites have been found to feed upon (Evans *et al.*,1961; Kevan, 1962; Crossley and Witkamp, 1964; Wallwork, 1967). They have also been found to serve as intermediate hosts for some cestodes (Freeman,1952; Allred,1954) and as vectors of various plant diseases (Sengbusch, 1954). Dowdy (1965) found species of *Allodamaeus, Tectocepheus, Trhypochthonius* and *Zercon* to be more abundant on the vegetation than in the soil during at least part of the year. It is perhaps worth noting that the mites associated with stored cereal products, including grain, (Sinha, 1963; 1964) constitute an entirely different fauna than those found in the soil. From the stand point of numbers of individuals and species diversification the roles performed by soil mites must be quite variable but important to the ecosystem.

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CALORIC VALUES OF SOME BOG LEPIDOPTERA[1]

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ABSTRACT

Caloric values of some of the more numerous Lepidoptera, that in one stage of their development have a soil-inhabiting phase, were measured with a bomb calorimeter. Values ranged from a low of 1.894 Kcal/g dry weight for the Geometrid *Eupithecia luteata* to a high of 9.546 for an Olethreutid *Eucosoma* sp. Caloric values for the various life stages of the green larch looper complex [Geometridae: Ennominae: *Semiothisa* prob. *sexmaculata* (Pack.)], one of the more common soil-inhabiting Lepidoptera, ranged from 0.002 Kcal for individual second instar larvae to 0.056 for individual pupa. The importance of these insects in the bioenergetics of the ecosystem is discussed.

INTRODUCTION

The life history, ecology, and population dynamics of the larch sawfly, *Pristiphora erichsonii* (Htg.), have been the subject of extensive and intensive investigation for many years (eg. Ives 1963, Ives and Nairn 1966, Lejeune 1955, Nairn *et al.* 1962). The major emphasis has been directed towards the population processes of the pest insect, but many parts of the ecosystem have been studied intensively, for example the avian complex in bog ecosystems (Buckner and Turnock 1965) and the small mammalian component of this fauna (Buckner 1958a, 1958b, 1966). The data collected in this program are applicable to ecosystem studies, and one such recent approach has been directed toward ecosystem bioenergetics (see Petrusewics 1967). The Lepidoptera constitute a large component of the soil biota, and are suspected of playing a major role in energy transfers of small forest vertebrates, particularly shrews and mice (Buckner 1964). Of these, the larch loopers of the *Semiothisa* Hu. complex comprise a significant component and are known to be used as food by both mammalian and avian predators (Buckner unpublished data). Consequently, a knowledge of the energy content of soil-inhabiting bog Lepidoptera is prerequisite to the understanding of energy flow through populations of the mammalian component of this system.

Many of the forest Lepidoptera pupate in the soil, and thus are vulnerable to predation by small mammals. The objective of this study is to ascertain the caloric value of the important lepidopterous groups and to relate this to biomass energy values.

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MATERIALS AND METHODS

Techniques for the measurement of larch sawfly populations in their various stages are now well developed (Ives *et al* 1968), and these techniques are readily adaptable to studying Lepidoptera as well. Adult emergence cages, useful in determining populations of adult larch sawflies, also collect large numbers of emerging Lepidoptera. These have provided a source of material for determining energy values as well as providing estimates of the emerging populations. In addition, larvae of the larch looper, *Semiothisa* sp., were hand collected: some were preserved for analysis as collected and others reared to various stages to provide material from a range of life stages as described by McGuffin (1947). All specimens destined for caloric determinations were dried for one week at 100°C at which time they had reached constant weight. Their caloric values were then determined in an Automatic Adiabatic Bomb Calorimeter. Individual specimens of all adult material, and of *Semiothisa* pupae were burnt in the bomb, but because of their small size only groups of larvae could be used for determining caloric values.

RESULTS

The number of emerging adult Lepidoptera was recorded on seven plots in which intensive studies on the larch sawfly were in progress. Adult Lepidoptera were collected from May to October in emergence traps sampling 2 sq ft of soil surface. Each plot contained 100 traps. The period of emergence ranged from early June to late October with the peak occurrence in July. Emerging Lepidoptera account for a significant portion of the total emerging bog insect fauna (Table 1), but the numbers of *Semiothisa* sp. among these were sporadic. Adult *Semiothisa* were collected from only four of the seven plots; Pine Falls, Hodgson, Telford, and Darwin. This insect comprised 92, 10, 5, and 2 per cent respectively of all emerging Lepidoptera in these sampling areas. Past records indicate that all plots support *Semiothisa,* and that the numbers of the insect range from very low to extremely high.

Caloric values of adult Lepidoptera ranged from a low of 0.003 Kcal for an unidentified Pyralidae to a high of 0.500 Kcal for an unidentified Phalaenidae (Table 2). The mean of all emerging adults was 0.098 Kcal which amounts to some 25,000 Kcal per acre in bog habitats. The families Noctuidae and Saturnidae yielded the highest caloric values per individual, and the family Gelechiidae the least (Table 3), which reflects the mean sizes of these groups. In terms of energy content per unit of weight, the Tortricidae and Gelechiidae yielded the least and the Olthreutidae the most. The Geometridae, which on the whole is the most numerous group in the bogs both in terms of numbers of species and frequency of occurrence, has a relatively low caloric content in terms of Kcal per individual and also per g dry weight. Special emphasis had been placed upon the energy values of *Semiothisa* sp., as it is one of the most numerous of the bog Lepidoptera and is likely to play an important role as a buffer for small vertebrate predators. It is unlikely that any stage below instar III would provide a major food source for small forest vertebrates, but the energy values of the later stages compare favourably with those of the other groups (Table 4). The highest energy value per individual is achieved in the pupal stage and the highest per g dry weight in the third instar.

DISCUSSION

Although knowledge of the energy values of the various components of the biota of an ecosystem are important to the understanding of the energetics and dynamics of the system, information on this aspect is scant. In selecting the Lepidoptera, we have attempted to gain some measure of one of the most numerous segments of the bog community. It is clear that prodigeous quantities of energy are contained in the lepidopterous component. It is further evident that *Semiothisa* sp. is likely to be at times, an acceptable alternative for predacious mammals. The *Semiothisa* component of the biomass is variable it is true, but at times it may comprise the bulk of the entire Lepidoptera component. With a pupal caloric value of

TABLE 1

The 1968 adult Lepidoptera populations of Manitoba bogs, compared with populations of larch sawfly adults.

Plot	Number of recovered adults*	Population/acre of adult Lepidoptera	Population/acre of sawfly adults
Rennie	31	29,403	23,740
Telford	22	11,415	165
Seddon's Corner	91	79,279	19,384
Pine Falls	37	29,839	4,574
Riverton	18	32,672	436
Darwin	64	58,153	18,949
Hodgson	10	27,225	5,663

* Numbers collected per season in 100 emergence traps each with a collecting surface of two square feet.

TABLE 2

Caloric values of the 1968 adult populations recovered from the emergence traps.

Family. Species, Subspecies	Dry weight/adult (g)	Kcal per adult	Kcal/g of dry wt
Arctiidae ..... (1)*	0.014	0.070	5.050
" , Hypoprepia ..... (1)	0.004	0.017	4.419
Gelechiidae ..... (1)	0.002	0.007	3.788
Geometridae ..... (1)	0.009	0.040	4.489
" , Anacamptodes vellivalata (1)	0.020	0.096	4.798
" , Endule mendica (1)	0.009	0.045	5.050
" , Eufidonia discospilata (2)	0.010	0.050	5.316
" , Eupithecia luteata (1)	0.004	0.005	1.262
" , Hypagyrtis piniata (1)	0.018	0.106	5.892
" , Isturgia truncataria (1)	0.004	0.007	1.894
" , Itame ..... (2)	0.006	0.037	6.313
" , Pero ..... (1)	0.044	0.252	5.739
" , Semiothisa prob. sexmaculata ..	See table 4.		
Nymphalidae, Euotoieta claudia (1)	0.025	0.131	5.252
Lycaenidae, Lycaena (3)	0.007	0.039	5.395
" , Lycaena (1)	0.007	0.053	7.575
Olethreutidae ..... (12)	0.0013	0.010	8.417
" ..... (60)	0.0011	0.006	6.413
" , Eucosma ..... (10)	0.0018	0.014	9.545
" , Olethreutes ..... (1)	0.0070	0.032	4.689
" , Pseudoexentera ..... (2)	0.0015	0.011	7.575
Phalaenidae ..... (1)	0.043	0.272	6.342
" ..... (2)	0.022	0.117	5.337
" ..... (1)	0.026	0.151	5.827
" ..... (1)	0.027	0.161	5.985
" ..... (1)	0.022	0.133	6.083
" , Agrotis ..... (3)	0.025	0.159	6.363
" , Autographa ..... (1)	0.028	0.197	7.034
" , Chorigagrotis ..... (2)	0.0585	0.315	5.395
" , Euxoa tessellata ..... (1)	0.025	0.141	5.656
" , Ochropleura ..... (1)	0.024	0.126	5.261
" , Orthosia hibisci ..... (1)	0.027	0.141	5.237
" , Polia ..... (1)	0.026	0.143	5.536
" , Protagrotis ..... (1)	0.036	0.257	7.155
Pyralidae ..... (2)	0.001	0.003	3.788
" , Argyria (2)	0.005	0.027	5.555
" , Carposina (1)	0.002	0.017	8.838
Saturnidae, Scepsis (4)	0.0263	0.159	6.060
Tortricidae ..... (1)	0.003	0.012	4.208
" , ... (1)	0.007	0.017	2.525
" , Archippus albertus (1)	0.003	0.007	2.525

* Numbers in parentheses represent the number of specimens analysed.

TABLE 3

The caloric values of adult Lepidoptera classified by family groups.

Family	Mean caloric value/ adult (Kcal)	Mean caloric value/g of dry weight (Kcal)
Arctiidae	0.044	4.735
Gelechiidae	0.007	3.788
Geometridae	0.066	4.602
Noctuidae	0.236	6.007
Nymphalidae	0.074	6.074
Olethreutidae	0.015	7.328
Pyralidae	0.016	6.060
Saturnidae	0.159	6.060
Tortricidae	0.012	3.086

TABLE 4

Caloric values of larch looper life stages of the *Semiothisa* complex, prob. *S. sexmaculata* Pack., Lepidoptera: Geometridae: Ennominae.

Stages	No. specimens	Individual wt (mg)		Percent water	Caloric values	
		Live wt	Dry wt		Kcal/individual	Kcal/g
Adult	37	5.09±1.43	4.37	14	0.023	5.26
1	0	—	—	—	—	—
2	3	—	0.40	—	0.0025	6.37
Larvae 3	11	—	0.75	—	0.0139	8.63
4	61	—	1.81	—	0.0107	2.55
5	94	—	5.14	—	0.0326	6.58
Whole pupae including cocoon	12	38.50±4.93	11.50	29±2	0.069+0.019	4.98
Pupae only	—	—	—	—	0.0565	5.40

TABLE 5

Biomass of the 1968 *Semiothisa* sp. populations.

Plot	Population/acre			Caloric values (Cal.)		
	adult	larvae 5	pupae	adult	larvae 5	pupae
Rennie	0	5,383	3,968	0	175.5	254.2
Telford	529	9,975	737	12.2	325.2	41.6
Seddon's Corner	0	4,277	1,623	0	139.4	91.7
Pine Falls	27,420	3,169	11,488	630.7	103.3	649.1
Riverton	0	21,902	5,578	0	714.0	315.2
Darwin	909	6,501	1,939	20.9	211.9	109.5
Hodgson	2,723	1,260	221	62.6	41.1	12.5

5.4 Kcal per g, it possesses approximately four times as great as the metablizable energy as an equivalent weight of larch sawfly eonymphs (Buckner 1964). An indication of the total calories available from *Semiothisa* sp. was derived from data collected in 1968 (Table 5), and although this year represented a low point in the population of this insect, nevertheless substantial energy values were afforded by it.

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