TOWARD INTEGRATED CONTROL

Proceedings of the Third Annual Northeastern Forest Insect Work Conference

New Haven, Connecticut
17 - 19 February 1970

U.S.D.A. FOREST SERVICE RESEARCH PAPER NE-194
1971

NORTHEASTERN FOREST EXPERIMENT STATION, UPPER DARBY, PA.
FOREST SERVICE, U.S. DEPARTMENT OF AGRICULTURE
WARREN T. DOOLITTLE, DIRECTOR

Proceedings of the Third Annual Northeastern Forest Insect Work Conference

CONTENTS

INTRODUCTION—*Robert W. Campbell* 1

TOWARD INTEGRATED CONTROL—
D. L. Collins 2

POPULATION QUALITY—
David E. Leonard 7

VERTEBRATE PREDATORS—
C. H. Buckner 21

INVERTEBRATE PREDATORS—
R. I. Sailer 32

PATHOGENS—*Gordon R. Stairs* 45

PARASITES—*W. J. Turnock and*
J. A. Muldrew 59

INSECTICIDES—*Carroll Williams and*
Patrick Shea 88

INTEGRATED CONTROL, PEST MANAGEMENT, OR PROTECTIVE POPULATION MANAGEMENT—
R. W. Stark 110

INTRODUCTION

by ROBERT W. CAMPBELL, USDA Forest Service, Northeastern Forest Experiment Station, Hamden, Connecticut.

ANY PROGRAM of integrated control is likely to be much more expensive than complete reliance on pesticides *in the short run*, especially if we restrict our thinking to the cost of program development. Clearly, the use of pesticides was more appealing in the years before publication of *The Silent Spring*. Not only did our operational systems consist primarily of one-dimensional pesticidal applications, but little research effort was devoted to the development of supplemental or alternative methods. DDT seemed to be a miracle remedy; that was all one had to know or care about!

Now a rising tide of public concern over possible adverse side effects of pesticides has resulted in increasing constraints on their use. And perhaps largely as a consequence of these constraints we are now beginning to see increasing adverse effects from the pests themselves. In the face of this, it seems both remarkable and tragic that we have yet to really face up to the increasingly urgent need to produce supplemental or alternative population-management systems.

Where do we go from here? First, we have to recognize that broad, flexible, and ecologically sound programs will not only cost a lot of money to develop but also that this development will take time. We then have to get this message across to a public that invariably wants action programs now! Second, we will have to plan ahead as carefully as possible. Scattered and uncoordinated research and control work usually result in findings that cannot be combined efficiently *a posteriori* to contribute to problem solution. Our efforts will have to be coordinated more closely in the future than they have been in the past.

TOWARD INTEGRATED CONTROL

by D. L. COLLINS

I HAVE a suspicion that the word "integrated" is one of the most overworked and misused terms in common circulation today, including its use when coupled with the word "control" with reference to insect pests. Therefore, before devoting an entire conference to the subject of "integrated control", we might do well to see if we know what it really means.

The word "integrated" is derived from the Latin adjective "integer", which originally meant "untouched" or "entire". When converted into a verb and then, with the past tense used as an adjective again—that is, the word "integrated"—its meaning according to Webster is: "composed of separate parts united together to form a more complete, harmonious, or coordinated entity".

For the word control we find several meanings, ranging from "power or authority to guide or manage" to "reduction or regulation of the wildlife population of an area by killing". Presumably the latter meaning conforms most closely to the interpretation commonly understood in the expression "integrated control".

If we substitute these definitions for the words we are defining, we come up with "reduction or regulation of the wildlife population of an area by killing (by use of) several separate parts united together to form a more complete, harmonious, or coordinated entity". Or, if we start fresh with the meaning of the word "integer", we would guess that integrated control would mean "complete control"—although this is not the way we usually understand it.

Thus we see that the common entomological meaning and the actual etymological meaning of the term are somewhat at variance. In spite of this semantic confusion, or perhaps even because of it, the expression "integrated control" has certainly caught on with the public as well as with entomologists. However, its ambiguity allows it to mean different things to different people, and therein lies a difficulty and danger. To a person confronted with an urgent pest problem, it is rather risky to recommend "integrated control", especially if you have to stay around and explain what you mean by it in terms of positive action to solve a particular problem. Yet, if we are to continue to use the expression, we must be prepared to accompany it with pertinent, useful advice. Otherwise the term becomes a fatuous subterfuge for avoiding the issue.

Possibilities

Historically, in forest entomology, or rather, in the control of forest insect pests, before the recent era of reliance on pesticides, the approach was basically one which we would now call "integrated". Such well-known and widely respected forest entomologists as S. A. Graham were emphasizing the suppression or regulation of forest pests by attention to certain biological facts and various cultural practices long before the term "integrated" began to be thrown around so loosely. Graham always emphasized means of control other than chemical, and I think we might well return to his early principles and precepts in an attempt to appraise the present situation.

Until recently it was thought by many persons, or at least hoped, that a control of the gypsy moth, or a way to stop its spread, could be developed in time to keep it from overrunning the southern and western Appalachian forests. Hence a belated, but intensive, almost desperate, effort to learn more about it, and to try anything that seemed to offer a chance of halting its advance. At about the same time that the program of total suppression and prevention of spread began to appear hopeless, the situation was further aggra-

vated by the furore about insecticides. Research on other possible control methods, which had already been under way, suddenly acquired stronger support, and many new possibilities received attention. A serendipitous result of the intensive work on gypsy moth has been the development of information that can also be applied to other forest pests as well.

A review of possible control methods for this insect would certainly include the following:

Release of sterile males.

Sex attractant pheromones.

Genetic manipulation.

Parasites.

Invertebrate predators.

Vertebrate predators.

Pathogens.

Feeding inhibitors.

Environmental manipulation.

Chemical pesticides.

Each of these methods has found a place somewhere in the control program for one or more pests. We all know, for example, of the use of the sterile males released against the screwworm, the use of lady beetles against scale insects in California, the use of *Bacillus thuringiensis* against cabbage loopers, and so on.

Unfortunately, each individual instance of success depends on a special set of circumstances that may be difficult or impossible to duplicate or approximate with some other species. This fact is often very difficult to get across to the public, who see this or that "new" technique as a breakthrough on old fronts. The sterile male technique, for example—or the use of specific pathogens and parasites—to be really workable may require that there be a practical way either to rear or to trap the insects in large numbers and to maintain continuous rearing or access to large natural populations. These procedures must be worked out separately for each species. They may include

the development of artificial foods and extensive and expensive greenhouse and insectary facilities manned by many persons with special training and duties.

Watchful Waiting

The economic factor is an important one, and one that in forest entomology problems is especially difficult to assess. The question "Is it worth the expense?" usually comes up eventually; and then we get into the realm of opinions and emotions and long-range effect, which makes it virtually impossible to give satisfactory answers—at least not without extensive applied research. Even with proven, if limited, success for a given control in a specific instance such as sterile males against screwworm or fruit fly, or virus against sawflies, or milky disease against Japanese beetle, we are on the defensive with every would-be control agency, whether it is a commercial applicator, a property owner, a garden club, or a public agency, unless, after we have said he can't or shouldn't spray, we can tell him something else to do that is really practical: where to get it, how to use it, or who can do it, and what to expect from it. Until we can do this, we are not very far along toward integrated control.

If we are honest, we have to admit that, with one or two exceptions, control of forest pests on a short-notice basis as a program with specific recommended steps is not now predictable with anything except sprays. Even with the exceptions, most of the measures that can be used require such exacting attention to technique and methods that they simply will not work except in the hands of specially trained personnel, and even then only under special conditions.

I think we are facing a long period of watchful waiting, in which, however, we must always be on the alert for a breakthrough. During this period, research will be continued and intensified. An occasional success will be hoped for, and will probably occur, and will certainly be needed to keep up enthusiasm, optimism, and support.

During this period we may learn that we do not need all the

control we thought we did. And since it is fairly certain we won't get it, the only thing we can do is to learn to live without it, and in the meantime to understand and encourage the natural control factors we have listed and any others that may be present, in any given situation. We may discover that what we really mean by "integrated control" is only the weighting of the balance of nature in what we consider to be a favorable direction. Our research programs are to help us increase these weights and show us how to apply them.

■

POPULATION QUALITY

by DAVID E. LEONARD
Department of Entomology, University of Maine, Orono, Maine

I AM CERTAIN that I do not have to convince anyone here that the quality of individual organisms can vary, and that individual differences can have a marked effect on the population biology of a species. In 1957, Wellington stated:

> "Populations are composed of individuals, and individuals differ. Nevertheless, our attempts to identify and evaluate the factors regulating animal numbers frequently seem to include a tacit assumption that the populations thus regulated are monolithic, or else consist of well-nigh interchangeable units that respond uniformly to given biotic or physical factors. Thus, students of population dynamics seldom determine the proportions of physiologically or genetically different groups within a generation or allow for the possibility that these proportions might change between generations as the population density changes."

This was the opening statement in Wellington's paper on individual differences as a factor in the population dynamics of the western tent caterpillar, *Malacosoma pluviale*. Although Franz (*1950*) and Chitty (*1957*) had hypothesized that differences in populations, particularly genetic differences, could affect the fate of populations, Wellington's studies were one of the first definitive works, showing that qualitative changes could influence the population dynamics of insects.

The effects of variations in population quality are probably best documented in the literature on small mammals, particularly microtine rodents. During the cycles of abundance of voles

and lemmings, many changes in population quality have been shown to affect the endocrine system, behavior, and reproduction. The mechanisms inducing these qualitative changes are either intrinsic, such as the effects of crowding, or changes in behavior; or they are extrinsic, such as differences in the quality or quantity of food.

Qualitative differences are known in insects. Phase polymorphism, density-related responses, many behavioral changes, and wing polymorphism can be a result of, or result in, differences in the quality of individuals. Differences in viability, fecundity, longevity, vigor, fitness—all of these can result from qualitative change.

I hope to demonstrate that:

- Population quality can be important in the dynamics of insect populations.
- Qualitative changes need not be based on genetically induced changes, as suggested by Chitty (*1960*), but may operate through induced physiological changes.
- Factors inducing qualitative changes can be considered in the formulation of techniques of pest management.

To show that individual differences in quality should be considered in understanding the population dynamics of a species, I will review briefly some of the work of Wellington on the western tent caterpillar, then will discuss my investigations of the gypsy moth, *Porthetria dispar* (L).

In 1957, Wellington showed that newly hatched caterpillars of the western tent caterpillar differed in their response to light. He was able to separate larvae into various categories according to their response. One component, called type I larvae, were the most responsive to light, ate more, and developed rapidly. A second component, called active type II larvae, were less responsive to light and developed slightly less rapidly than the most active component. The third component, called sluggish type II larvae, developed slowly and often fed less because they spent more time in the tent. In rearings, when type I or type I and active type II larvae were combined, the colony was vigor-

ous; but when pure type II larvae were reared, survival was poor. Adults showed the same pattern of activity as the larvae from which they came. More active larvae produced more active adults, which were more vigorous fliers and dispersed to establish new and distant infestations. Thus new infestations consist initially of active colonies, and these active colonies are characterized by the elongate shape of their tents.

Gypsy Moth Work

When I started to work with the gypsy moth, I decided to concentrate my efforts on determining whether a similar intrinsic mechanism might be operating and masking the attempts to explain, on the basis of abiotic factors, the causes of the population fluctuations common to this defoliating lymantriid. These population flushes can be very dramatic. They occur mostly on the higher elevations containing favorable host trees, primarily species of oaks.

In the Northeast, the gypsy moth problem involves more than damage to a cash timber crop. In recreation areas, gypsy moth outbreaks seriously curtail their use. Furthermore, many people who live in the suburbs, which are frequently wooded, object to sharing their ecosystem with other organisms, particularly insects. Pressure (often political) is applied to "solve the gypsy moth problem". The continued quest for immediate solutions does not provide a suitable situation for sustaining the biological and ecological investigations necessary to prevent or even predict outbreaks. As a result, after 100 years, and expenditures of tens of millions of dollars, we know little more about the gypsy moth than the information published by Forbush and Fernald before the turn of this century.

It is difficult to work in the laboratory with insects that require fresh foliage, and a wheat germ diet was modified for gypsy moth larvae (*Leonard and Doane 1966*). I wanted next to determine the rate of development of larvae on the diet, at the temperature and light regimes to be used in subsequent studies—16 hrs. photoperiod per 24-hr. day, and 23.5°C. About 60 larvae were isolated at hatch and reared individually in petri

dishes. They were checked each day; the frass was removed for drying and weighing; and the day of each molt was recorded. When the larvae were in what I thought should be the last larval stage—the 5th instar in males and the 6th in females—it was apparent that some larvae were going to molt again: to a 6th instar in males and a 7th in females. Of the 58 larvae reared, 26 had an additional stadium (*Leonard 1966*).

A check of the literature showed that the occurrence of an additional instar was known for this species, at least since the studies of Fernald (*1896*).

I probably would have not considered the occurrence of an additional molt further had I not data to compare those larvae with "normal" larvae. These differences in gypsy moth larvae that have undergone an additional instar (*Leonard 1966*) are outlined below:

1. Prolonged instar I, with longer prefeeding phase.
2. Prolonged development to adulthood.
3. Increase in pupal weight (fecundity).
4. Shortened pupal stage.

Additional Molt

I didn't realize it at the time, but with these data I had uncovered the response to a qualitative change that functions as a self-regulating mechanism as the gypsy moth population density increases. If you will accept for a few moments that the occurrence of an additional molt is evidence of a response to a qualitative change, I would like to discuss how this response can be triggered, before discussing the importance of the qualitative change in the population biology of the gypsy moth.

Additional larval stadia can be induced during early larval development: (1) crowding (*Leonard 1968*), (2) starvation (*Leonard 1970a*), and (3) cool temperatures (*Leonard 1968*).

The crowding experiments were conducted not to determine the effect on the number of molts, but rather to check the effects of crowding on the rate of development. In field populations, adults are often found 1 to 2 weeks earlier in dense populations than they are in sparse ones. To determine the effects

of crowding on the rate of development, about 800 larvae were crowded; and these were compared with about 200 larvae that were reared in isolation (*Leonard 1968*). The rates of development were recorded in such a manner that it was possible to reconstruct the molting records for each larva in the crowded cultures. When these data were compared with those from larvae reared in isolation, these effects of crowding gypsy moth larvae (*Leonard 1968*) appeared:

1. Prolongation of instar I, followed by a more rapid rate of development in subsequent instars.
2. Lower pupal weight.
3. Increase in the number of larvae with an additional instar.
4. Lighter coloration of adult males.

The rate of development to adulthood in crowded cultures was faster than in isolated ones, but the increased rate was not a generalized increase in all instars. In instar I, the rate of development was slower, whereas in instars II, III, and IV the rate of development was faster. In both sexes, the duration of the pupal period was shorter, even though on pupation all pupae were isolated one per 1-oz. plastic cup.

As one might expect, the pupal weights of crowded larvae were lower; in females, about 35 percent lower, and in males, 20 percent lower. Maksimovic (*1958*) has shown that pupal weight and fecundity are correlated in this species.

The number of additional larval stages in the crowded cultures was higher:

Test	*Larvae with additional instar*	
	Isolated (percent)	*Crowded (percent)*
1	8.9	23.1
2	39.5	51.7

This increase was obtained even though the level of crowding during instar I, when this trait apparently is induced, was relatively low.

Another interesting result of crowding was a change in the coloration of adults. Unlike the conventional cases of phase polymorphism, the crowded individuals were lighter.

Starvation experiments were conducted to determine if starvation, by extending the length of the 1st instar, could induce an additional molt. Larvae starved during the 1st instar had a significant increase in the number of subsequent molts:

Days not fed	*Larvae tested* (*No.*)	*Additional molt* (*percent*)
1 & 2	130	33.1
3 & 4	138	32.6
5 & 6	141	31.2
Control	141	14.1

Larvae starved in a similar manner during instars II, III, and IV did not show an increase in the number of additional molts. In fact, starvation early in these instars resulted in a consistent trend toward a reduction in the number of additional molts, providing some evidence that this trait is reversible during later instars.

Study of Egg Masses

Although the qualitative change, expressed as an increase in the number of larval instars, can be induced by factors that delay development during instar I, it is of more importance to the population biology of this species that this trait can be induced during the previous generation through the egg (*Leonard 1970b*). To determine the frequency in occurrence of additional molts, a sample of or all of the progeny of 87 egg masses have been analyzed. In each of the 87 egg masses, some larvae underwent an additional molt, with the range in additional molting types from 2.7 to 97.9 percent. This range of difference was not due to differences in rearing techniques, since all larvae were reared individually, on the same diet, in the same controlled room. Thirty-five egg masses had up to 20 percent of their progeny with one or more additional molts, whereas 14 egg masses had over 80 percent of their progeny with one or more additional molts.

It would appear at first that the maternal influence might be a genetic trait, but crossing experiments between different molting forms could establish no tendency for the trait to segregate

as a Mendelian gene, even though Goldschmidt (*1934*) stated that the trait was regulated by alleles of the "T" gene.

Pursuing the egg-additional molt relationship further, I divided six egg masses into equal quarters according to their basal area, from front to rear. The eggs from each quarter were dehaired, then measured with an occular micrometer. Each egg was allowed to hatch, the larvae were reared to pupation, and the number of molts were recorded. Two interesting pieces of data emerged:

- There was a size gradient in eggs, from the front to the rear of the egg mass, with the first eggs laid and the first produced in the ovaries of the females being larger.
- There was a higher percentage of additional molting types in the last quarter of the egg mass.

In four of the six egg masses analyzed, the increase in larvae with an additional molt from the smallest eggs was from just under twofold, to more than a threefold increase. In the two egg masses in which no such trend was observed, the percentage of additional molting types was very high in all quarters of the egg mass.

The relationship of small egg size and the increase in the number of instars indicated that there was most likely a correlation with nutrition of the eggs, since the smaller egg size probably signified a smaller amount of yolk content. About the time that I was completing these studies, Wellington and Maelzer (*1967*) published a paper on the results of their experiments on the western tent caterpillar, treating pupae with farnesyl methyl ether, a juvenile hormone mimic. The developing eggs in treated pupae were deprived of nutrients, and these eggs produced a higher percentage of the sluggish behavioral types, indicating to the authors that the behavioral types in *M. pluviale* are mainly nutritional products. Also, Wellington (*1957*) had shown earlier that the sluggish larvae had a higher tendency to have an additional larval molt.

Differences in Dispersal

To determine if eggs from sparse gypsy moth populations differed from those from dense field populations, egg masses have been fragmented into quarters, and the eggs measured. In the egg masses from the sparse population, the first eggs laid were the largest. In the egg masses from the dense population, the number of eggs per mass was much smaller, and although the same tendency of the first egg laid to be larger is seen, the range of difference in the size of eggs from the first to last portion of the mass was less. Also, the eggs tend to be smaller than those from the sparse field population. The eggs from the dense population were more like those from the last quarter of the egg mass in the sparse population. These eggs have not yet been reared to determine the number of larval instars, but one could predict from earlier work that the numbers of additional molting types will be higher in these eggs than from those of the dense field populations.

I have spent much time establishing that the gypsy moth has a qualitative change expressed in an additional larval instar, but I have not yet indicated what effect this change has on the population biology of the species. The extra-molting types differed in several ways. Any of these differences could have a marked effect on the population biology of the gypsy moth, but I would consider that the most important difference is the prolonged rate of development during instar I. This life stage is perhaps the most critical of all; for after hatching, larvae must leave the egg mass and find suitable food. Of importance to the evolutionary biology of this species is that instar I is the only stage in which dispersal can effectively take place. Female gypsy moths are flightless. The dispersal of larger larvae can be measured in meters, but the spread of newly hatched larvae can be measured in miles.

Any factor prolonging the first instar will enhance the possibility of dispersal—but this is only partially true. It is the behavior of larvae that has the most important impact on dispersal. During instar I, larvae normally remain on the leaves. They spend most of their time on the undersides, and come to the

top surface to feed at dawn after temperatures reach 45°F. (*Leonard 1970*). Larvae return to the undersides of leaves in mid to late morning, and a few will again feed in the afternoon. At night, larvae are on the undersides of leaves. While on the undersides of leaves, larvae are anchored to a sparse mat of silk, and they are not readily dislodged. Also, after their first meal, their weight doubles. These quiescent larvae are not likely to be dispersed, and few larvae trapped on screens have the characteristic appearance of having fed (*Leonard 1967, in press*).

If larvae hatch where there is no food, as on dead trees or other inanimate objects, they become more active as hunger increases. Easily irritated, these larvae are induced to spin down on a thread of silk (*Leonard 1967*). These larvae are readily picked up and dispersed by even a slight breeze.

The larvae that hatch from small eggs—those that undergo the qualitative change—have a longer prefeeding phase, during which they will not settle and feed, even in the presence of suitable food. The prolonged instar I is a reflection of this longer prefeeding phase. In dense field populations, I have collected and released larvae at the base of saplings and recovered only a few (*Leonard, in press*). The larvae climbed the sapling, encountered leaves with no larvae on them, yet continued climbing to the top of the sapling, or the tip of the branches, and were dispersed. These larvae hatched from nutritively deficient eggs showing characteristic signs of hunger. What finally induces such larvae to settle and feed is not yet known.

Dispersal is passive, and few larvae will be deposited where suitable food is available. Those larvae that do survive, because of their additional larval stage, have higher pupal weight and are more fecund. Part of the loss encountered in dispersal is offset by a higher reproductive potential of survivors.

Population Flush

The gypsy moth is characterized by population flushes. These flushes, on the surface, appear to be deleterious, for they ultimately result in dramatic crashes when the food resources

are depleted, and/or epizootics occur. I suggest that these flushes are a necessary event in the biology of the gypsy moth to bring about dispersal and genic mixture. If one can visualize a hypothetical population in an area where suitable host plants prevail, one would anticipate that the population density would increase, with the rate of increase dampened by various biotic and abiotic factors. As the population density increases, there comes a point in a gradation where larvae are stressed, and these larvae produce the females that lay eggs with reduced food reserves.

The larvae emerging from these eggs will not readily settle and feed, but remain in an active state, which greatly enhances their chances for dispersal by wind. Before the population crashes, many larvae will have been dispersed. Thus population flushes can be advantageous to insure dispersal and genetic recombination, and may have evolved with the loss of flight in females. This mechanism of self-regulation provides the gypsy moth with the means of reacting to changing environmental conditions, particularly increasing population densities, both more rapidly and more efficiently than if this mechanism were under strict genetic control and dependent on selection for its expression. This is an important point, one that has been overlooked by many who consider that qualitative changes must operate as Mendelian systems. It is not necessary to select out ninety-nine percent of the gypsy moths to have this functional polymorphism operate.

It would be interesting to know at what density nutritively deficient eggs will be produced during a population flush. I would predict that it is the density at which there is an observable and dramatic shift in the diel periodicity of larval activity. For the first three instars, larvae commence feeding with the first light of morning, as temperatures moderate. At instar IV there is a dramatic shift in feeding behavior: larvae feed during hours of darkness and remaining quiescent during the day. At high population densities, this diel periodicity is upset, and larvae are active both day and night. This shift occurs before there is any obvious lack of available food. I feel that it is these active larvae that are producing the smaller eggs, for they prob-

ably spend less time feeding, and their wandering behavior utilizes food reserves that would normally be deposited in the eggs.

What particularly intrigues me is that all elements of this qualitative change—the deficient eggs, the change in diel periodicity, the change in larval behavior at instar I, and the increase in the number of larval molts—could all be controlled by the same hormonal system, the brain-corporus allatum-prothoracic gland system. Certainly molting is controlled by this hormonal system. DeWilde (*1964*) reviewed work showing that the corporus allatum affects the amount of proteid yolk supplied the trophocytes during oogenesis, and also affects feeding behavior in some insects. Wellington and Maelzer (*1957*) treated pupae of the western tent caterpillar with a mimic of juvenile hormone, and obtained eggs deprived of nutrients.

Can the occurrence of a density-regulated mechanism to induce dispersal be used to effect control of the gypsy moth? I believe it can, by preventing this qualitative change from taking place. Such a strategy would necessitate a completely different approach to control. At present, dense populations are sprayed by air to prevent defoliation. In the post-DDT era, this procedure is not as effective, for the short-residual insecticides don't provide the same protection as did DDT.

During a gypsy moth outbreak, the windspread of larvae creates several problems. Larvae are dispersed to new areas, and most of the spread of this insect throughout the Northeast has been by this means, and the spread westward is hampered primarily by the prevailing winds in the spring. Larvae are also spread in large numbers into the areas adjacent to the outbreak, often into areas where they would not normally occur in troublesome numbers.

Strategy

The strategy I suggest is to monitor gypsy moth populations only in areas of potential foci of epidemics—mainly on the higher elevations. When these populations begin to increase to the point where the qualitative shift and subsequent dispersal would occur, then some means of control would have to be applied.

This would occur while the population was still sparse, before any noticeable defoliation had taken place. Because of this, the whole concept of control would be different, for it would not be necessary to attain a high percentage kill; in fact, it would be disadvantageous, for in a population-management strategy, it would be desirable to maintain as many biotic control agents as possible.

As far as I know, no one has attempted to maintain sparse gypsy moth populations. If such an approach were to be initiated in the near future, it would probably be necessary to use insecticides, for too little is yet known about the use of biotic agents. Many insecticides are not now considered for use because they do not perform well against outbreak pupulations. These insecticides may be useful in a population-management scheme, with the residual population serving as a reservoir of biotic control agents. The areas to be sprayed would be greatly reduced, and the woodlands in the lower elevations would be ignored, because the populations in these areas rarely reach outbreak conditions unless there is a large influx of dispersing larvae.

There are a number of biotic control agents that could be useful in maintaining sparse gypsy moth populations, including parasites and predators. Some of these species might be suited for mass culture for release to suppress gypsy moth populations. There are two diseases that are promising: the nuclear-polyhedrosis virus, and the strain of *Streptococcus faecalis* recently discussed by Doane and Redys (*in press*). Both of these pathogens have given encouraging results in field applications (*Rollinson et al. 1965; Doane in press*).

The sterile-male technique, which has apparently been hampered by rearing problems, has not yet been tested adequately.

The sex pheromone of the gypsy moth female provides several novel alternatives for control.

None of the biotic control agents has been noted to provide adequate control, but they were expected to perform against epidemic populations, where numbers of gypsy moths were often so high that a small percentage of survivors could still cause defoliation. In a population-management approach to control,

defoliation will not be a concern, and abiotic agents, either singly or in concert, could provide a means of preventing outbreaks.

In summary, the quality of insects comprising populations may be an important factor in the biology of that population. In the gypsy moth, qualitative changes occur primarily as a response to increasing density, and appear to be characterized by a nutritive change affecting the physiology of the insect, particularly the hormonal system. A major response to the qualitative change is an increase in dispersal. Such a density-regulated mechanism to induce dispersal can operate more rapidly and efficiently than one with direct genetic links that depends on selection for its expression. Preventing such a qualitative change by maintaining populations at sparse levels may make it possible to prevent widespread epidemics. Such a strategy would necessitate a change in the current concepts of pest control, and would require a thorough knowledge of the population biology of both the target insect and the biotic control agents.

Literature Cited

Chitty, D.
1957. SELF-REGULATION OF NUMBERS THROUGH CHANGES IN VIABILITY. Cold Spring Harb. Symp. Quant. Biol. 22: 277-280.

Chitty, D.
1960. POPULATION PROCESSES IN THE VOLE AND THEIR RELEVANCE TO GENERAL THEORY. Can. J. Zool. 38: 99-113.

Doane, C. C.
[In press.] FIELD APPLICATIONS OF A STREPTOCOCCUS CAUSING BRACHYOSIS IN LARVAE OF PORTHETRIA DISPAR. J. Invert. Pathol.

Doane, C. C., and J. J. Redys.
[In press.] CHARACTERISTICS OF MOTILE STRAINS OF STREPTOCOCCUS FAECALIS PATHOGENIC TO LARVAE OF THE GYPSY MOTH. J. Invert. Pathol.

DeWilde, J.
1964. REPRODUCTION — ENDOCRINE CONTROL. *In* The physiology of Insecta 1, Rockstein (Ed.). pp. 55-90. Acad. Press, New York and London.

Fernald, C. H.
1896. THE GYPSY MOTH, PORTHETRIA DISPAR (L.) PART II. *In* The Gypsy Moth, *Porthetria dispar* (Linn.). 495 pp. Wright and Potter, Boston.

Forbush, E. H.
1896. THE GYPSY MOTH, PORTHETRIA DISPAR (L.) PART I. *In* The Gypsy Moth, *Porthetria dispar* (Linn.). 495 pp. Wright and Potter, Boston.

Franz, J.
1950. ÜBER DIE GENETISCHEN GRUNDLAGEN DES ZUSAMMENBRUCHS EINER MASSENVERMEHRUNG AUS INNEREN URSACHEN. Z. Angew. Entomol. 31: 228-260.

Goldschmidt, R.
1934. LYMANTRIA. Biblio. Genet. 11: 1-185.

Leonard, D. E.
1966. DIFFERENCES IN DEVELOPMENT OF STRAINS OF THE GYPSY MOTH, PORTHETRIA DISPAR (L.). Conn. Agr. Exp. Sta. Bull. 680: 1-31.

Leonard, D. E.
1967. SILKING BEHAVIOR OF.. THE GYPSY MOTH, PORTHETRIA DISPAR (L.). Can. Entomol. 99: 1145-1149.

Leonard, D. E.
1968. EFFECTS OF DENSITY OF LARVAE ON THE BIOLOGY OF THE GYPSY MOTH, PORTHETRIA DISPAR (L.). Ent. Exp. & Appl. 11: 291-304.

Leonard, D. E.
1970a. EFFECTS OF STARVATION ON BEHAVIOR, NUMBER OF LARVAL INSTARS, AND DEVELOPMENT RATE OF PORTHETRIA DISPAR. J. Insect Physiol. 16: 25-31.

Leonard, D. E.
1970b. INTRINSIC FACTORS CAUSING QUALITATIVE CHANGES IN POPULATIONS OF PORTHETRIA DISPAR (L.). Can. Entomol. 102: 239-249.

Leonard, D. E.
1970. FEEDING RHYTHM IN LARVAE OF THE GYPSY MOTH. J. Econ. Entomol. 63:1454-1457.

Leonard, D. E.
[In press b.] AIR-BORN DISPERSAL OF LARVAE OF THE GYPSY MOTH AND ITS INFLUENCE ON CONCEPTS OF CONTROL. J. Econ. Entomol.

Leonard, D. E., and C. C. Doane.
1966. AN ARTIFICIAL DIET FOR THE GYPSY MOTH, PORTHETRIA DISPAR (L.) (LEPIDOPTERA:LYMANTRIIDAE). Ann. Entomol. Soc. Amer. 59: 462-464.

Maksimovic, M.
1958. EXPERIMENTAL RESEARCH ON THE INFLUENCE OF TEMPERATURE UPON THE DEVELOPMENT AND THE POPULATION DYNAMICS OF THE GYPSY MOTH (LIPARIS DISPAR L.). Posebno Izdanje Bioloskog Inst. NR Srbije 3. [Trans. from Serbo-Croatian 1963. OTS 61-11203: 1-95.]

Rollinson, W. D., F. B. Lewis, and W. E. Waters.
1965. THE SUCCESSFUL USE OF A NUCLEAR-POLYHEDROSIS VIRUS AGAINST THE GYPSY MOTH. J. Invert. Pathol. 7: 515-517.

Wellington, W. G.
1957. INDIVIDUAL DIFFERENCES AS A FACTOR IN POPULATION DYNAMICS: THE DEVELOPMENT OF A PROBLEM. Can. J. Zool. 35: 293-323.

Wellington, W. G., and D. A. Maelzer.
1967. EFFECTS OF FARNESYL METHYL ETHER ON THE REPRODUCTION OF THE WESTERN TENT CATERPILLAR, MALACOSOMA PLUVIALS: SOME PHYSIOLOGICAL, ECOLOGICAL, AND PRACTICAL IMPLICATIONS. Can. Entomol. 99: 249-263.

■

VERTEBRATE PREDATORS

by C. H. BUCKNER, Canadian Forestry Service,
Chemical Control Research Institute, Ottawa, Ontario

THE ROLE of small vertebrates as predators of forest insects has not been widely studied. Nonetheless, in those instances where this aspect of the population dynamics of forest insect pests has been examined there is substantial evidence that further investigation would be profitable. To appreciate fully the role of vertebrates in an integrated control system, we first of all should examine the role of vertebrates in the forest ecosystem. Next we should examine their impact upon insects of economic importance. And finally we should examine means of employing the knowledge gained into meaningful integrated management schemes. I use the word vertebrates synonymously with only the higher taxa; in other words, birds and mammals.

Vertebrates in the Forest Ecosystem

When we examine the vertebrate fauna of a forest system as predators on forest insects, we can reduce a vast array of taxonomic groups to a few dozen. Of the birds, the forest entomologist would be interested in the wood warblers, the fringilids, and the woodpeckers. Among the mammals, he would be interested in the insectivores and rodents. And it would be only fair to point out that these groups bear relationships on both the plus and minus sides of the ledger; for although they do destroy forest insects in significant numbers, some of their other behaviours tend to counterbalance the beneficial effects of their predatory habits. For example the woodpeckers, although they destroy prodigious numbers of noxious insects, also drill tap holes that injure trees and damage forest products. And rodents that in general are surprisingly efficient insect predators, also de-

stroy seeds, seedlings, and saplings that could extend the economic benefits of the forest.

Unlike the parasitoids that usually have a relatively restricted range of types of prey, most forest vertebrates consume a wide array of food material. They are also in general highly discriminate in their choice of foods, and their choice may not always be in the interests of control of a specific noxious pest. On the other hand, they may respond to population increases of a specific insect to the advantage of the forest manager.

For example, when abundant, the spruce budworm forms a significant component in the diets of many forest birds (*Morris et al.* 1958), and the larch sawfly is fed upon almost exclusively by certain small avian predators during periods of abundance (*Buckner and Turnock 1965*). This response very frequently continues below the level of the effectiveness of certain parasites, which has prompted Morris and associates to point out that at low levels of budworm populations it may in fact be the vertebrate portions of the forest fauna that are exerting the controlling influence upon this insect.

In the sawfly-infested bogs of southern Manitoba it has been shown that the larch sawfly is a preferred food of many of the small mammals inhabiting the ecosystem and that their predation often is the most significant of all biological control elements within the system (*Buckner 1966*). Alternatively, however, it has been pointed out that there are indeed very few vertebrate predators of insects such as the forest tent caterpillar and the gypsy moth, both of which appear to have strong defences against possible predation by vertebrate predators (*Buckner 1966*). These defences presumably are olfactory and tactic in nature and tend to reduce the effectiveness of a potential vertebrate predator population. Data about this are very scarce, and what is required is a much wider description of the foods and feeding habits of as many vertebrates in the ecosystems that are of interest to us as we can manage to assemble.

Selective feeding behaviours of small forest vertebrates play an important role in their ultimate role in the population dynamics of any insect. We should take care to assemble as much information as we can on this interesting aspect of our problem.

For example, many birds are known to avoid diseased insects. Some diseased insects are obviously unpalatable to avian predators. Others, having been attacked for example by certain parasites, become so irritable that they make difficult targets for avian predators. Thus larch sawflies that have been discoloured by disease or those that exhibit the thrashing movements of irritability following attack by parasites are rarely consumed by small warblers and fringilids that are foraging amongst the branches. And in the realm of small mammalian predators of forest insects there is now considerable evidence that many insects that have been attacked by parasites are no longer palatable to small mammalian predators. Mammals tend to reject larch sawflies parasitized by diptera and disease to a greater extent than those parasitized by hymenoptera.

In addition to the direct effects of attack by vertebrates on insect individuals, there are also subsidiary feeding behaviours which tend to increase the predation pressure upon an insect population. For example, certain birds feed only upon a portion of their insect prey (*Buckner and Turnock 1965*). Certain sparrow predators of the larch sawfly decapitate the larvae and feed only upon the head. Some of the grosbeaks decapitate their larvae and feed only upon the thoraxic portion. Other predators break their prey in two and consume only a part, and still others destroy their prey without ever feeding upon it.

Small mammals also exhibit subsidiary feeding behaviours. For example, shrews kill insects apparently for the sport of it. Most mammals gather and hoard large quantities of insect prey to feed upon later when most prey are unavailable in their natural state. There are, of course, some counterparts of this in the attacks of invertebrate predators and parasitoids of forest insects. For example, certain hymenopterous parasites sting without ovipositing; and stung prey, because they usually die, are destroyed in a subsidiary manner. Frequently destruction of prey through the subsidiary processes are of greater importance than attack for the satisfaction of basic food requirements. Insects such as the larch sawfly suffer more through the effects of subsidiary feeding behaviours than they do to satisfy the basic food requirements of their predators (*Buckner 1966*).

The numerical strength of predators is also of importance in determining their relationships in the population dynamics of forest insect pests. It is only rarely that small forest vertebrate populations are closely tied to the population abundance of insect prey. Small vertebrate populations are more frequently linked with complexities in the biological ecosystem.

For example, breeding populations of small song birds are almost assuredly limited by their territorial behaviour. An upper limit may be reached far below the carrying capacity of the environment in which they exist. Certain small mammals such as the aggressive shrews also exhibit territorial behaviour, and the upper limit of their breeding populations are almost certainly limited by this factor. Available nesting sites both for small mammals and birds also form an important component of the population dynamics of these groups.

There is, however, a response by small vertebrate predators that may be directly related to the numerical strength of the prey. This is effected through behavioural responses rather than by strictly breeding ones. There are many examples of small vertebrates aggregating in areas where prey densities are high. Elton (*1942*), for example, describes a congregation of tawny owls moving into an area in which voles have increased in numbers; and of course the control of the mormon cricket by gulls is a striking classic example of a behavioural numerical response.

In the realm of forest insects there are also a number of examples. Blais and Parks (*1964*) have indicated that residual populations of the spruce budworm have been almost certainly controlled through the predatory actions of the grosbeaks that have invaded the remaining pockets of infestation after insecticide treatment; and Buckner and Turnock (*1965*), working on the larch sawfly, have demonstrated quite clearly that birds that do not normally inhabit the bog ecosystem range into the bogs for feeding in times of larch sawfly abundance. There is also evidence that small mammalian cocoon predators invade the bogs from upland sites when large numbers of cocoons are forming in the late summer.

These examples, although not fitting the classic idea of nu-

merical responses, are nonetheless effective numerical responses in the population dynamics of a particular pest species; and, it has been pointed out, many of these responses are of greater significance in the population dynamics of the pest than are the classic breeding responses as first outlined by Solomon *(1949)*. For the pest insect it matters very little whether the response has arisen through breeding or through an aggregation of independent individuals moving into the area to feed on an abundant prey.

The Impact of Vertebrate Predation

Reliable estimates on the impact of small vertebrate predators on populations of forest insect pests are very rare indeed. This factor has been neglected in sophisticated analyses on the population dynamics of the major pest insects. However, a few examples indicate that there is promise in this line of investigation.

The studies of R. F. Morris *et al. (1963)* on the spruce budworm populations in central New Brunswick undoubtedly provide the best long-term continuing records on this aspect. Morris and associates have assessed populations of small mammals and birds in budworm-infested stands for almost two decades and have concluded that, in general, small mammals play an insignificant role in the dynamics of budworm populations, but that considerable importance may be attributed to the role of small birds as predators of this insect, especially at low insect densities. Morris *et al. (1958)* have considered small birds as possibly one of the major controlling factors at endemic prey levels. Watt *(in Morris 1963)*, deriving his information from Morris' long-term data, also advocates that birds may be of considerable importance in cleaning up residual populations of the past after the major outbreak has run its course. These data are substantiated by Blais and Parks *(1964)*.

Neilson and Morris *(1964)*, working on the European spruce sawfly, have also attributed vertebrate predation as a key factor in the population dynamics of this insect. Small mammal predators acting upon the cocoon stage are probably the most important controlling factor of this insect.

In independent studies of winter moth population fluctuations, Embree *(1965)* in New Brunswick and Varley and Gradwell *(1962)* in England concluded that small mammals preying upon the pupal stages of this insect can be a very important population mechanism indeed. The Canadian studies have indicated that small mammals—particularly shrews—are likely to play an exceedingly important role in the population dynamics of this insect, but that their depredations are overshadowed by insect parasites, which in this particular pest insect account for a higher proportion of mortality than do small vertebrate predators.

Essentially the same situation occurs in the winter moth infested oak forests in Britain, where Varley and Gradwell arrived at similar conclusions except that the extent of mammalian predation is somewhat higher than the situation in Canada and the insect parasites somewhat lower. However, on this insect, control is very likely effected by the combination of both factors, and the balance is attributed primarily to invertebrate control measures rather than small vertebrates.

Similar studies on this insect in the USSR *(Korol Kova 1963)* have indicated that small song birds are important predators of this insect and could account for a considerable proportion of the total mortality. Many of the Russian workers attribute a greater importance to the role of small avian predators than they do to small mammals. Chief among the mammal predators both in Europe and Asia and in North America are the shrews, and these account for considerable numbers of winter moth.

MacLeod *(1966)* and associates, working on the jack pine sawfly in Quebec, have investigated the role of small mammals as cocoon predators. This research team has attributed considerable importance to the predatory effects of small mammals, particularly shrews. They have noted that vast quantities of sawfly cocoons have been destroyed by these small predators and that this may be a key factor in the dynamics of this insect.

The team approach to study of the larch sawfly in central Manitoba has taken into consideration the role of small vertebrates in the population dynamics of this insect. Continuing records of small vertebrate populations on a number of the perma-

nent study plots now range back almost two decades. It has been concluded from the analyses of these population data that small song birds, as in the case of the spruce budworm, may be of considerable importance in the population dynamics of the larch sawfly. Their importance is likely greater at low than at high insect population densities.

There are several striking responses to the prey population when it reaches higher densities, however; and these are affected through large numbers of avian predators invading the bogs and destroying large quantities of insects. In general, one must conclude that their effect is greatest at lower insect densities. Studies on small mammals concurrent with those on birds, and reaching back in the continuum several years farther, have indicated that these are likely the most important population decimating agent acting against the larch sawfly in this area.

The effects, however, are exceedingly erratic. At some times mammals destroy large numbers of the cocoon population, and at others they destroy relatively insignificant numbers. This erratic effect produces erratic fluctuations, and it must be concluded that mammals in general certainly are not the perfect key factors that one would have hoped for. However, they do serve as important subsidiary population-controlling mechanisms and should be considered seriously in management programs.

The Integrated Approach

In considering small vertebrates in insect pest management programs, one must point out that to date no real integrated approach to control, specifically using small vertebrates, has ever been attempted. The remarks that follow therefore represent a few ideas as to how one might consider these in an overall control program. I would like to bring forth as the example the effect of mammals and birds as predators of the larch sawfly.

The most important single group of vertebrate predators of the larch sawfly are the shrews. There are six major insectivore predators of the larch sawfly in the tamarack bogs of southeastern Manitoba. These are the cinereus shrew *Sorex cinereus*, the saddle-backed shrew *Sorex arcticus*, the water shrew *Sorex*

palustris, the pigmy shrew *Microsorex hoyi*, and the short-tailed shrew *Blarina brevicauda*.

These six species occur in varying numbers and in varying microhabitats within stands infested by the larch sawfly. The most catholic in distribution is the cinereus shrew which ranges from the central water edge well up to the upland sites. The most restricted is the water shrew, which is confined principally to the fringes of the water areas. The others to a greater or a lesser degree range in limited areas throughout the remainder of the habitat. The saddle-backed shrew inhabits the deeper yet drier areas of the bogs. The pigmy shrew occupies the transitional zone between bog and upland. The short-tailed shrew, principally an upland species, invades to some extent the drier areas of the bog. From the standpoint of numbers, we can consider only four of them as important predators: the cinereus shrew, the saddle-backed shrew, the pigmy shrew, and the short-tailed shrew. The cinereus shrew is most important of all.

The cinereus shrew and the pigmy shrew consume the largest quantities of insect material. The cinereus shrew indeed feeds almost exclusively on the larch sawfly during periods when the insect is abundant. Curiously, however, the cinereus shrew feeds principally on larvae extracted from the cocoons; whereas the pigmy shrew feeds more on adult insects and hence destroys larger quantities of adult insects. The saddle-backed shrew, although it has a larger appetite because it is larger, consumes a smaller proportion of insect material; it feeds both on larvae and on adults. The short-tailed shrew, although almost half its diet consists of insect material, is not a particularly important predator of the larch sawfly because the sawfly accounts for only about 15 to 20 percent of its total diet.

The selectivity of the various shrews also bears importance. For example, the cinereus shrew rejects cocoons that have been attacked by fungus, by decay, or that have been attacked by dipterous parasites. When selecting parasites for release against an insect such as this one, one should, all other things being equal, favor dipterous over hymenopterous parasites because of the selective feeding behaviour.

In the propositions so far put forward to control the larch

sawfly, one of the most promising proposals has been a treatment whereby the water table in infested stands is manipulated. The principle behind this is that, when cocoons are newly formed or are going into the transition in forming adults, they are extremely susceptible to inundation. Thus if we were able to flood newly formed cocoons or cocoons that were in the process of transforming into adults, perhaps we could effect good control. This may also effect the shrew populations, for the saddle-backed shrew requires a relatively deep water table whereas the habitat requirements of *Sorex cinereus* are considerably less restrictive. Thus we could not only favor selection of a desirable shrew species, but also could couple this with a very devastating inundation of the developing cocoons.

By raising the level of the water table we would at the same time favor the more desirable cinereus shrew; and if such a flooding operation were effected during a period at which the shrews were reproducing, this would increase the possibility of favoring cinereus and at the same time decrease the abundance of the less desirable saddle-backed shrew. And if at the same time we could lower the water table at a time when sawflies are falling from the trees, we could perhaps increase the population of the saddle-backed shrew to take advantage of its larger appetite. So by careful manipulation of the water table we might not only effect the devastating direct blow against the sawfly but couple this with a heavy impact from shrew predators.

Under circumstances in which a chemical control might be considered, we should also be cognizant of the toxicity of the proposed chemical treatment to small forest vertebrates. Certain chemicals are more toxic to small rodents than they are to small insectivores. The choice of a chemical could increase the chances of impact upon the forest pest by decreasing the rodent population, thus allowing an upswing in the insectivore population, which would then add its impact to that of the chemical on the pest insect.

So far, I have considered only the insectivore component of the vertebrate system, but there are a number of other small vertebrate predators that could be effective. Of the other mam-

mals in the system, the small red-backed vole, *Clethrionomys gapperi*, is not only the most numerous but also the most insectivorous. Depredations by this species certainly augment the impact effected by the shrews. Both the cinereus shrew and the red-backed vole hoard cocoons and consume them later when food is scarce. The response of the shrew resembles the disc curves described by Holling *(1959)*, whereas the response of the rodent is more complicated, rising to a maximum but then decreasing again at the higher densities. The effectiveness of such an impact has a relatively narrow range.

And finally, the avian component of the predator system is also important. Spring breeding populations, particularly of the warblers, establish and stabilize relatively early; and the later seasonal fluctuations probably represent increment and migratory movements. Weak numerical responses to gradients of the pest populations are evident, but the greatest numerical responses are behavioural ones. Most of the bog-inhabiting or bog-foraging avian species are effective predators of the target insect, but some feed primarily on larvae, others principally on adults, and still others about equally on both.

So in considering an integrated approach and evaluating the small vertebrates concerned with such an approach we should consider first of all the type of predator that we wish to encourage. Surely we want one with a high feeding capacity, one that has a preference for the target insect, one that is reticent to feed upon insects attacked by other natural control agents acting against that insect, one that maintains high population densities, one that can respond quickly to other control measures applied simultaneously, and one that will be relatively unaffected by subsidiary treatments. One example of such a predator is certainly the cinereus shrew, and it is significant that this is one of the first vertebrates ever to be experimented with for controlling a forest insect. The case I am referring to is, of course, the introduction of *S. cinereus* into Newfoundland to add to the biological control complex of the larch sawfly (*Buckner 1966*). The shrew now occupies much of the island and causes a significant impact upon the pest insect.

References

Blais, J. R. and G. H. Parks.
1964. INTERACTION OF EVENING GROSBEAKS (HESPERIPHONA VESPERTINA) AND THE SPRUCE BUDWORM (CHORISTONEURA FUMIFERANA (CLEM.)) IN A LOCALIZED SPRUCE BUDWORM OUTBREAK TREATED WITH DDT IN QUEBEC. Can. J. Zool. 42: 1017-1024.

Buckner, C. H.
1966. THE ROLE OF VERTEBRATE PREDATORS IN THE BIOLOGICAL CONTROL OF FOREST INSECTS. Ann. Rev. Ent. 11: 449-470.

Buckner, C. H. and W. J. Turnock.
1965. AVIAN PREDATION ON THE LARCH SAWFLY, PRISTIPHORA ERICHSONII (HTG.) (HYMENOPTERA: TENTHREDINIDAE). Ecol. 46: 223-236.

Elton, C.
1942. VOLES, MICE AND LEMMINGS: PROBLEMS IN POPULATION DYNAMICS. Oxford, Clarendon Press.

Holling, C. S.
1959. SOME CHARACTERISTICS OF SIMPLE TYPES OF PREDATION AND PARASITISM. Can. Entomol. 91: 385-397.

Korol'Kova, G. E.
1963. VLIYANIE PTITS NA CHISLENNOST' VREDNYKH NASEKOMYKH. Akad. Nauk. SSSR (Engl. trans. in library Can. For. Serv., Ottawa).

McLeod, J. M.
1966. THE SPACIAL DISTRIBUTION OF COCOONS OF NEODIPRION SWAINEI MIDDLETON IN A JACK PINE STAND. I. CARTOGRAPHIC ANALYSES OF COCOON DISTRIBUTION WITH SPECIAL REFERENCE TO PREDATION BY SMALL MAMMALS. Can. Entomol. 98: 430-447.

Morris, R. F. (Ed.)
1963. THE DYNAMICS OF EPIDEMIC SPRUCE BUDWORM POPULATIONS. Ent. Soc. Can. Mem. 31: 332 pp.

Morris, R. F., W. F. Cheshire, C. A. Miller, and D. G. Mott.
1958. THE NUMERICAL RESPONSE OF AVIAN AND MAMMALIAN PREDATORS DURING AGRADATION OF THE SPRUCE BUDWORM. Ecol. 39: 487-494.

Neilson, M. M. and R. F. Morris.
1964. THE REGULATION OF EUROPEAN SPRUCE SAWFLY NUMBERS IN THE MARITIME PROVINCES OF CANADA FROM 1937 TO 1963. Can. Entomol. 96: 773-784.

Solomon, M. E.
1949. THE NATURAL CONTROL OF ANIMAL POPULATIONS. J. Anim. Ecol. 18: 1-35.

Varley, G. C. and G. R. Gradwell.
1962. THE INTERPRETATIONS OF INSECT POPULATION CHANGES. Ceylon Assoc. Adv. Sci. Proc. 18, (II): 142-156.

■

INVERTEBRATE PREDATORS

by R. I. SAILER, Entomology Research Division, USDA
Agricultural Research Service, Beltsville, Maryland

OF THE TWO WORDS that comprise my subject, each in a different way presents a problem. Zoologically the *invertebrates* include about every animal organism that cannot be classified as vertebrate. However, for purpose of discussion my comments will be restricted to arthropods and more specifically to the classes Insecta and Arachnida. The term *predator* is no less troublesome, for it is virtually impossible to accurately categorize the trophic behavior of many invertebrate species. Though it would be convenient to pigeonhole each species as phytophagous, parasitic, predacious, saprophytic, etc., this becomes a practical impossibility in the face of dietary habits that change from one life stage to another.

For example, what is one to do with a species such as *Itoplectis conquisitor* (Say). This hymenopterous insect develops as a pupal parasite of the gypsy moth. However, the adults may kill and feed on body fluids of as many as 250 pupae for each pupa successfully parasitized (*Campbell 1963*). When not stinging host pupae for feeding or oviposition, the adult female will feed, together with the adult males, on aphid honeydew and flower nectar.

The number of species exhibiting this type of parasitic behavior is very large. One family alone is estimated by Townes (*1970*) to contain 60,000 species. This would of course be the Ichneumonidae. Many years ago Wheeler (*1923*) coined the term *parasitoid* and applied it to these insects, which he regarded as not true parasites, but as extremely economical predators. Although in the past not generally accepted by entomologists, the term now seems likely to come into common usage. With

the resurgent interest in biological control, there is need for a term that can be applied to the parasitic insects that will not convey the more restricted connotation and often opprobrious meaning of parasite.

However, the introduction and use of the term parasitoid points up my problem in discussing invertebrate predators. If I am to talk about the significance of predation by one insect on another, I can scarcely overlook the predatory activity of a very large number of parasitoid species.

Few people with any degree of familiarity with insects fail to be impressed by their remarkably diverse feeding habits. Certainly almost any conceivable dietary habit or combination of habits will be exhibited by one or more species of insect. However, I question whether even entomologists fully appreciate the extent to which the predacious habit pervades the insect world. If we were to list all orders, families, tribes, and genera of Insecta and Arachnida containing species that are predacious in some life stage, few groups above the tribal taxon would be omitted.

When we view invertebrates in terms of number of kinds and diversity of habit, it is obvious that a really conscientious treatment of invertebrate predators could profitably occupy much more than my allotted time. Therefore I propose to speak in generalities and to venture little more than some opinions regarding the role of predators in the population dynamics of prey species.

The Terms

So there be no misunderstanding about my use of terms when referring to different habits of insect groups, I will comment on distinctions between the terms *predator, parasitoid,* and *parasite.* Most people will agree that a predator is an organism that normally kills a more or less large number of serially contacted and consumed prey organisms. A parasite by contrast will live most of its life permanently attached to a single living host.

Unfortunately, the above definition of a parasite ill describes the behavior of most parasitic insects. Many species commonly

referred to as parasites actually develop in hosts that are either killed by the parent parasite or die at some point in the development of the invading organism. Such parasitic insects are also usually free-living in the adult stage and in this stage may behave as predators.

Therefore, in further discussion of the importance of predators as compared with parasitoids and pathogens, remember that predacious activity of parasitoids will contribute to the functional importance of predation.

As indicated earlier, my principal objective is to consider the respective roles of predation, parasitism, and disease in regulation of host populations. Ultimately the question becomes one of knowing how these agents are to be manipulated for the purpose of holding pest populations at or below economic thresholds.

In 1929 W. R. Thompson wrote that though insect predators are numerous and are generally acknowledged to be beneficial, they are by no means universally believed to be as useful and important as insect parasites. Thompson then proceeded to present his reasons for believing that the part played by predacious insects was under-estimated. He argued that the relative importance of these two types of controlling agencies in any given case could be decided only by careful investigations in the field. Despite the recent life-table studies and mathematical models of R. F. Morris (*1963*), K. E. F. Watts (*1959, 1963*), C. S. Hollings (*1959, 1963*), and others it is my impression that our understanding of the relative role of predators in regulating pest populations has not advanced greatly beyond that of 1929. Perhaps it would be more correct to say that our ability to modify ecosystems through manipulation of predator populations has not advanced appreciably.

Though I make no pretense of being an active research worker in this field, I have for some 10 years now been involved in one way or another with biological-control programs. As a result of recent developments with which you are all well acquainted, biological control has suddenly moved from an almost stagnant backwater into the main current of research on pest control. Questions that could once be safely relegated to the

ivory tower are now being hotly debated even in the popular press. Program-management people are finding such questions relevant and are pressing research personnel for answers that will not be immediately forthcoming.

Among the questions for which answers are needed, one of the most important is that of the relative values of the three major categories of natural enemies. If predators, parasitoids, and pathogens play different roles in regulating host populations, we must know what these roles are and how each can be used to the best advantage in the strategy of pest management. As a result of my own field experience and general familiarity with entomological research, I am convinced that invertebrate predators are very much more important than is generally realized. In fact I think there is good reason to believe that they constitute our first line of defense against the onslaught of insect pests.

The Value of Predators

Certainly we have examples that amply illustrate the potential value of predators. The first and most publicized example of biological control, the cottony-cushion scale, was accomplished by a predator—the vedalia beetle. Another coccinellid (*Cryptognatha nodiceps* Marshall) has controlled coconut scale (*Aspidiotus distructor* Signoret) in Fiji (*Taylor 1935*) and Principe (*Simmonds 1959*). A different kind of predator, the mirid bug *Cyrtorhinus mundulus* (Breddin), controlled the sugar cane leafhopper *Perkinsiella saccharacida* Kirkaldy in Hawaii (*Pemberton 1948*).

There are many well-documented cases of population release among previously innocuous plant-feeding species of insects and mites following use of organic insecticides. This is generally attributed to destruction of both predators and parasitoids. Evidence of this was reported by Hoffmann et al. (*1949*), who noted massive outbreaks of the mite *Paratetranychus ununguis* (Jac.) and several species of aphids in a Pennsylvania forest experimentally treated with DDT in 1945. They attributed these outbreaks to elimination of the abundant mite predator *Coniopteryx vicina* Hagen and drastic reduction of such aphid pred-

ators as *Anatis 15-punctata* (Olivier) and several species of syrphid flies.

Later examples of secondary pest problems that have followed in the wake of DDT and similar highly effective insecticides are too numerous and well known to warrant citing here. The likelihood that these problems have been precipitated in great part by the destruction of natural enemies is indicated by excellent experimental evidence. Perhaps the most convincing of the experimental studies are those of Franz (*1958*) and DeBach (*1955*). Franz was able to demonstrate highly significant increases of the balsam woolly aphid, *Adelges piceae* Ratz, in "plot" areas of tree trunk from which predators were excluded. DeBach used the insecticidal check method and concluded that DDT residues had no direct or indirect benefical effect on a diaspine scale population except through selective elimination of parasitoid *Aphytis chrysomphali* (Mercet). It is also well known that many scale insect and aphid outbreaks result from ants protecting them against predators and parasitoids (*DeBach, Dietrick and Fleschner 1951*).

From these various lines of evidence I believe most people are now willing to agree that natural enemy populations constitute a valuable stabilizing influence in ecosystems and are important factors in control of many pests. However, there is no general agreement about, or great interest in, the relative importance of predators, parasitoids, and pathogens as separate components of the natural enemy complex. Such comparisons as have been made have, for the most part, concerned the comparative ability of individual species to control pest populations. Any assessment of the value of predators as opposed to parasitoids or pathogens has consisted of little more than a tally of pests controlled by one as opposed to another. It is important that this question be investigated, for it may have great bearing on how natural enemies are managed.

Three Approaches

On the basis of present knowledge, there are three possible approaches to the use of predators and parasitoids for pest control:

1. The introduction of effective enemy species into niches where there are unexploited or inefficiently exploited food resources in the populations of pest species.

2. Modification of the environment to provide conditions favorable for increase of enemy species already present and able to exploit the pest populations.

3. The mass-production and inundative release of species capable of feeding on and destroying pest populations before they cause economic damage.

Of these approaches the first two impress me as the most practical and in the long run the least expensive. This is particularly true of pest problems associated with the forest habitat. Many of you know of the work that is being done in Europe and the USSR to utilize ants for control of certain forest pests. A summary of the European literature on this subject was published by G. Cotti in 1963. Other important references are one by K. Gösswald, G. Kneitz, and G. Schirmer in 1965 and an evaluation of the European research on use of red wood ants for protection of forests published by K. G. Adlung in 1966. That similar use of ants is being made in the USSR is indicated by papers published in the proceedings of a 1964 Symposium on Biological Control of Agricultural and Forest Pests edited by A. I. Cherepanov.

In Italy, under the direction of M. Pavan, extensive efforts have been made by the ministry of Agriculture and Forestry to relocate colonies of *Formica polyctena* Foerst in pine forests. As a result of a census conducted by 1,500 agents of the Italian State Forest Corps, Pavan (*1959*) calculated that in the Italian Alps there were more than 1,000,000 nests of four species of *Formica*. He estimated that these nests contained 300 billion workers that would destroy 14,400 tons of insects during an annual activity period of 200 days.

In Germany Gösswald (*1940*) has developed techniques for mass-breeding queens of *Formica rufa* F., and he has investigated the economic value of these ants. He has also actively promoted the colonization of ants in many forest situations for

control of sawflies and lepidopterous pests. Ant hills are protected by law in Italy, Switzerland, and Germany; and I have been told by a German colleague that our military forces in Germany are billed for each ant hill destroyed in the course of maneuvers or other activities.

In Russia, Smirnov (*1964*) recommended that hills of the genus *Formica* be moved from forests that are being cut and placed in new plantations. Marikovskii (*1964*) noted that it was futile to move colonies to forests where competing species of ants were already well established. He urged that until more information was available and better success obtained from efforts to colonize the red wood ants, first priority should be placed on protection of existing colonies by means of State regulations and public education.

Adlung (*1966*) noted in his review clear evidence that ants are of value in controlling the common European forest pest *Panolis flammea* (Schiff.), and that the species *F. polyctena* has a certain limited value in pine forests. He concluded that establishment of nests is of no value in spruce plantations and would be injurious in beech forests, where the ants would protect and promote outbreaks of aphids that in turn cause the trees to be attacked by a canker fungus. He also noted that a considerable part of the ant's prey consists of beneficial insect species. Hence it may be concluded that ants are not an unmixed blessing even in situations where they do exercise effective control over pest populations.

An Appalling Task

There are of course many other examples of manipulation of predators, most involving movement of species from one country to another. In view of the number of pests that have invaded new continental and insular areas as well the certainty that predator species in many areas could be replaced by more efficient species resident in other areas, there is no doubt that much can be done to alleviate pest problems through introduction programs.

However, as a one-time taxonomist who has had some experience with insect ecology and its applied phase, biological con-

trol, I am appalled by the magnitude of the task that confronts entomologists if we seriously undertake to find and intelligently utilize all the invertebrate predators that are of potential value. There are thousands of species, a very large number of which are not even known to systematic entomologists. We need to know where to find these species and to know details of their life cycles, their ecological requirements, and what we might call their performance specifications. This boils down into a vast inventory job, supported by an information storage and retrieval system that would enable us to quickly determine what species of predator is available and capable of controlling a pest at a place where control is desired. In my opinion our present resources are totally inadequate to meet such a challenge.

The second approach is one that is almost equally formidable. It would require changes in agricultural practices and silviculture on a scale that would require many years if not decades to accomplish. At present we can only guess at what is possible. It is also questionable whether, in the face of the demands for food and space for our human population, the method would be economically feasible. Basically this approach constitutes the most important element of what is being referred to as integrated control or pest management. Although much talked about and experimentally demonstrated to be effective in California (*Stern et al. 1959*) the method has been purposely applied in only a few places and then on a limited scale. The most outstanding of these are applications in Nova Scotia against apple pests (*Pickett et al. 1958*) and in Peru against cotton pests (*Simon 1954*) and cocoa pests in Malaysia (*Conway 1969*). However, the dates of the first two suggests that there has been no great rush to put into practice what has been loudly preached in recent years.

The third method is one that offers promise of being effective in dealing with at least some pest problems. In the case of certain high economic return crops it may prove feasible to control pests by inundative or innoculative release of suitable predators. I am aware that most past efforts to use this technique have been unsuccessful. However I am encouraged by the results of a 1968 experiment conducted in Texas by R. L. Ridg-

way and S. E. Jones (*1969*). In this experiment two field releases totaling 292,000 *Chrysopa carnea* Stephens larvae per acre reduced the populations of *Heliothis zea* (Broddie) and *H. virescens* (F.) by as much as 96 percent and increased the yield of cotton in the test plots threefold. However, a word of caution is in order. The practical application of this method, even for control of *Heliothis* on cotton, will require extensive research on timing of release, numbers required, and most of all upon development of efficient and economical methods of mass-production and distribution of the predator.

Opportunities

I hope my comments will not be construed as presenting an unnecessarily pessimistic picture. Even with our present resources there are opportunities for significant progress toward solution of at least some of our pest problems through manipulation of predators. Furthermore, there is reason to believe that, within an ecosystem, predation acts as one of the most important factors in maintaining stability of the system. There are several lines of evidence suggesting that this is the case.

As a group, predators tend to be less specific in their food habits than parasitoids. They are less dependent upon a single food resource and are better able to maintain stable populations that tend to exploit prey species in proportion to their relative abundance. They also tend to be longer-lived and less likely to be adversely affected by physical factors of their environment. Their searching capabilities are generally greater, and in cases where a predator tends to be specific in its food habits there is likely to be a compensatory increase in either its fecundity or in its searching capacity. These are all characteristics that make predators well suited to play a specialized role in the regulative processes that restrain prey populations to levels below the carrying capacity of their habitat.

Nicholson (*1933*) Utida (*1955*) and others have experimentally confirmed the mathematically derived conclusion that interaction between a host and a parasite within a closed system results in population fluctuation of each species in oscillations of

ever-increasing amplitudes to the point of mutual extinction. That such extinction rarely if ever occurs in nature is attributed by Voûte (*1951*) to the delayed-density-dependent action of predators. This action dampens the oscillations otherwise inherent in the host-parasite relationship. The direct effect is not so much on the prey population, but rather is due to intervention in the relationship between the prey and its parasites. The result is that the populations of both prey species and parasite are regulated at a more or less stable level. Voûte referred to this as "the quenching principle."

More recently Flanders (*1963*) has studied the interactions of food, prey, phytophage, predator, parasitoid, and pathogen components of an ecosystem. Within his system, Flanders found it necessary to introduce shelters that provided the phytophage a degree of protection "above the threshold of security" in order to maintain stability. This is clearly an example of Voûte's "quenching principle," and it introduces the element of space and shelter into population dynamics. However, of special interest to me was Flanders' evidence that disease epizootics occurred in his system followed elimination of the predator by periods of starvation due to host scarcity.

This sets the stage for what I suggest is a plausible and potentially useful classification of phytophagous arthropod populations and their associated natural enemies. In the tabulation that follows, populations are arranged in the order of four levels of abundance reflecting progressively increased density relative to carrying capacity of the habitat. The dominant regulative factor characteristic of each level is also shown:

Class	*Effect on ecosystem*	*Regulating factor*
1	Harmonic	Predators
2	Intrusive	Parasitoids
3	Disruptive	Pathogens
4	Catastrophic	Food

Though the above classification is grossly simplified, it is consistent with a very large body of empirical evidence derivable from the literature and experience of economic entomologists. However, examples will immediately come to mind that would seem to refute validity of such a classification. Perhaps the most striking is that of the Japanese beetle, *Popillia japonica*

Newman, a pest that is now generally believed to be regulated over large areas at a non-economic level by the pathogen *Bacillus popilliae* Dutky (*Fleming 1968*).

I regard the Japanese beetle as an exception that will tend to support the rule. Here the "quenching principle" function is provided by the characteristic habitat of the beetle larvae. The soil in which the larvae live provides a habitat in which the long lived *Bacillus* spores accumulate to a point where probability of non-infection is so high that few larvae survive to become adult. Obviously there are many other exceptions of a similar nature as well as examples that will doubtless exhibit almost every conceivable combination of two or more regulative factors working in conjunction. However, as a generalization that might serve as a useful guide for planning the strategy of biological control and pest management, such a classification could be most useful.

In any event I would urge that greater attention be given to the research on factors responsible for regulating non-economic populations. In the past entomologists have spent a disproportionate amount of time studying threatening or outbreak populations. We know little about what is happening to pest species during intervals between outbreaks or in areas where they are non-economic. If the role of invertebrate predators is a regulative factor responsible for restraining phytophagous insect populations to a harmonic part of their ecosystem, it would follow the biological control experts should place highest priority on the protection and augmentation of predacious species.

References

Adlung, K. G.
1966. A CRITICAL EVALUATION OF THE EUROPEAN RESEARCH ON USE OF RED WOOD ANTS (FORMICA RUFA GROUP) FOR THE PROTECTION OF FORESTS AGAINST HARMFUL INSECTS. Zeitschrift fur Angewandte Entomologie 57: 167-189.

Campbell, R. W.
1963. SOME ICHNEUMONID-SARCOPHAGID INTERACTIONS IN THE GYPSY MOTH PORTHETRIA DISPAR (L.) LEPIDOPTERA: LYMANTRIIDAE. Can. Entomol. 95: 337-345.

Cherepanov, A. I. (Ed.)
1964. BIOLOGICAL CONTROL OF AGRICULTURAL AND FOREST PESTS. Academy of Sciences USSR, Siberian Branch. Symp. 17-20 November, Proc. 1964: 179 pp. Novosbirsk. Translation by S. Nemchomok 1969 (available U.S. Dep. Commerce Clearing house for Federal and Technical Information Springfield, Virginia, 22151.)

Conway, Gordon R.
1969. A CONSEQUENCE OF INSECTICIDES. Natural History, Special Suppl., Conf. Ecol. Aspects Int. Develop. Programs. Dec. 6-11, 1968. Warrenton, Virginia.

Cotti, G. 1963.
BIBLIOGRAFIA RAGIONATA 1930-1961 DEL GRUPPO FORMICA RUFA IN ITALIANO, DEUTSCH, ENGLISH. MIN. AGR. FOR. Collana Verde 8, Rome. 413 pp.

DeBach, Paul E. J. Dietrick and C. A. Fleschner.
1951. ANTS VERSUS BIOLOGICAL CONTROL OF CITRUS PESTS. Calif. Citograph 36: 312, 347-348.

DeBach, Paul.
1955. VALIDITY OF THE INSECTICIDAL CHECK METHOD AS A MEASURE OF THE EFFECTIVENESS OF NATURAL ENEMIES OF DIASPINE SCALE INSECTS. J. Econ. Entomol., 48: 584-588.

Flanders, S. E. and M. E. Badgley.
1963. PREY-PREDATOR INTERACTIONS IN SELF-BALANCED LABORATORY POPULATIONS. Hilgardia 35(8): 143-183.

Fleming, W. E.
1968. BIOLOGICAL CONTROL OF THE JAPANESE BEETLE. USDA Tech. Bull. 1388, 78 pp.

Franz, J. M.
1958. THE EFFECTIVENESS OF PREDATORS AND FOOD IN LIMITING GRADATIONS OF ADELGES (DREYFUSIA) PICEAE (RATZ.) IN EUROPE. 10th Int. Congr. Entomol. Proc. (1956) 4: 781-787.

Gosswald, Von. K., G. Kneitz and G. Schirmer.
1965. DIE GEOGRAPHISCHE VERBREITUNG DER HUGELBAUDEN FORMICA ARTEN (HY., FORMICIDAE) IN EUROPE. Zool. Jb. Syst. 92: 368-404.

Hoffman, C. H., H. L. Townes, H. H. Swift and R. I. Sailer.
1949. FIELD STUDIES ON THE EFFECTS OF AIRPLANE APPLICATIONS OF DDT ON FOREST INVERTEBRATES. Ecol. Monogr. 19: 1-46.

Holling, C. S.
1963. SOME CHARACTERISTICS OF SIMPLE TYPES OF PREDATION AND PARASITISM. Can. Entomol. 91: 385-398.

Holling, C. S.
1963. AN EXPERIMENTAL COMPONENT ANALYSIS OF POPULATION PROCESSES. Entomol. Soc. Can. Mem. 32: 22-32.

Huffaker, C. B.
1958. EXPERIMENTAL STUDIES ON PREDATION: DISPERSION FACTORS AND PREDATORS-PREY OSCILLATIONS. Hilgardia 27: 343-383.

Marikovskii, P. I.
1964. SOME PROBLEMS INVOLVED IN THE UTILIZATION OF ANTS FOR PROTECTION OF FORESTS AGAINST INSECT PESTS. See Cherepanov 1964, pages 129-131. loc. cit.

Morris, R. F.
1963. PREDICTIVE POPULATION EQUATIONS BASED ON KEY FACTORS. Entomol. Soc. Can. Mem. 32: 16-22.

Nicholson, A. J.
1933. THE BALINCE OF ANIMAL POPULATIONS. J. Animal Ecol. (Suppl.) 2 (1): 132-178.

Pavan, M.
1959. ATTIVITA ITALIANA PER LA LOTTA BIOLOGICA CON FORMICHE DEL GRUPPO FORMICA RUFA CONTRO GLI INSETTI DANNOSI ALLE FORESTE. Min. Agr. For. Collana Verde 4: 1-80. Rome.

Pemberton, C.E.
1948. HISTORY OF THE ENTOMOLOGY DEPARTMENT EXPERIMENT STATION, H.S.P.A. 1904-1945. Hawaiian Planters Rec. 52: 53-90.

Pickett, A. D., W. L. Rupman and E. J. LeRoux.
1958. PROGRESS IN HARMONIZING BIOLOGICA' AND CHEMICAL CONTROL OF ORCHARD PESTS IN EASTERN CANADA. 10th Int. Congr. Entomol. Proc. (1956) (3): 169-174.

Ridgeway, R. L. and S. E. Jones.
1969. INUNDATIVE RELEASES OF CHRYSOPA CARNEA FOR CONTROL OF HELIOTHIS ON COTTON J. Econ. Entomol. 62: 177-180.

Simon, F. J. E.
1954. SOME EXPERIMENTS ON CONTROL OF COTTON PESTS: INTERPLANTED CORN AND SYSTEMATIC INSECTICIDES. Inf. Estac, Exp. Agric. LaMolina No. 90. 22 p., illus. Lima.

Simmonds, F. J.
1959. BIOLOGICAL CONTROL—PAST, PRESENT, AND FUTURE. J. Econ. Entomol. 52: 1099-1102.

Smirnov, B. A.
1964. UTILIZATION OF ANTS IN PROTECTION OF FORESTS. see Cherepanov 1964, pages 152-154, loc. cit.

Stern, V. M., Smith, R. F., Van Den Bosch, R. and Hagen, K. S.
1959. THE INTEGRATION OF CHEMICAL AND BIOLOGICAL CONTROL OF THE SPOTTED ALFALFA APHID. PART I. THE INTEGRATED CONTROL CONCEPT. Hilgardia 29: 81-101.

Taylor, T. H. C.
1935. THE CAMPAIGN AGAINST ASPIDIOTUS DESTRUCTOR SIGN. IN FIJI. Entomol. Res. Bull. 26: 1-102.

Thompson, W. R.
1929. ON THE RELATIVE VALUE OF PARASITES AND PREDATORS IN THE BIOLOGICAL CONTROL OF INSECT PESTS. Entomol. Res. Bull. 19: 129-144.

Townes, H.
1969. THE GENERA OF ICHNEUMONIDAE. PART I. Amer. Entomol. Inst. Mem. 11, 300 pages. Ann Arbor, Michigan.

Voûte, A. D.
1951. ZUR FRAGE DEN REGULIERUNG DER INSEKTENPOPULATIONSDICHTE DURCH RAUBERISCHE TIERARTEN. Zeit. f. ang. Entomol. 33: 47-52.

Watt, K. E. F.
1959. A MATHEMATICAL MODEL OF THE EFFECT OF DENSITIES OF ATTACKING SPECIES ON THE NUMBER ATTACKED. Can. Entomol. 91: 129-144.

Watt, K. E. F.
1963. MATHEMATICAL POPULATION MODELS FOR FIVE AGRICULTURAL CROP PESTS. Entomol. Soc. Can. Mem. 32: 83-91.

Wheeler, W. M.
1923. SOCIAL LIFE AMONG THE INSECTS. 375 pp. Harcourt, Brace and Co. New York.

■

PATHOGENS

by GORDON R. STAIRS, Faculty of Entomology, College of Biological Sciences, Ohio State University, Columbus, Ohio

MANIPULATION OF THE environment of insect species often results in the species becoming a pest. There are many examples of this, such as monoculture of crops and forests.

Most species of insects are very adaptable, so that the least disruption of the general environment may cause great changes in population densities. The changes may be either increases or decreases. An increase in population is observed more often because it may be manifested by an increase in damage to a crop. A decrease in population may go unnoticed, but it may be ecologically important to know the causes of the decrease.

Crop losses are usually money losses; so attempts are made immediately to control the pest. Several routes may be followed, but the easiest (and least expensive) is the application of chemical poisons. The use of chemical poisons has been the main means of controlling most insect pests during the last 25 years. The construction of a spray-calendar has been the main occupation of most entomologists because use of chemicals was, and still is, the cheapest, simplest, and easiest way to ensure farmers minimum crop loss to insect pests.

Because it is the easiest, cheapest, and simplest, it is not necessarily the best. The best of anything usually costs more, so we should be careful not to introduce control practices that may provide questionable long-term esthetic, financial, and monetary returns. We know we should be managing our renewable resources more efficiently, particularly in the face of ever-increasing people populations; but policy changes are complex and difficult to effect.

The forest industries of this country are probably leading in this respect because detailed plans for management of large tracts of forested land must be approved by appropriate control agencies. There is a positive effort to provide increased supplies of wood on a sustaining basis without unduly disrupting the environment. A similar approach will eventually have to be developed for many of our food commodities. The agriculturist should be turning even now to the forester to set the patterns for the management of renewable food resources. The principles in both areas are essentially the same in that we are dealing with organisms growing on the surface of the earth.

The ecosystem is not *ad infinitum* as may appear on superficial examination. Individual organisms differ in size, form, etc.; but there are many more similarities than once was thought. We might say that the systems are so highly integrated that one influences the other either directly or indirectly. We must not overlook this principle when studying insect populations or recommending control procedures. Indirect long-term effects may be more important to society than apparently good short-term, monetary, and esthetic returns. This is the approach we are advocating in the study and utilization of pathogens of insects for the suppression and regulation of pest populations.

For best results we should have complete knowledge, but we should be able to make better and better decisions as we gather more and more data. The decisions we have to make should determine the kinds of data we obtain. In the case of pathogens, we know that viruses, bacteria, fungi, protozoa, and nematodes cause disease in insects, including many species that are regarded as pests (*Steinhaus 1949*). In many instances, pest population declines have been associated with disease outbreaks or epizootics (*Balch and Bird 1944*; *Bird and Elgee 1957*; *Bergold 1951*); and there are several examples of the successful dissemination of pathogens for the suppression of pest populations and even the artificial initiation of epizootics (*Briggs 1963*; *Bucher 1958*; *Dutky 1959*; *Heimpel and Angus 1960*; *Steinhaus and Thompson 1950*; *Clark and Reiner 1946*; *Stairs 1964*). However, the practical use of pathogens for pest control and population regulation is in a very early stage of development.

Information Needed

Information concerning the qualitative incidence of pathogens is being collected, but very few studies of a quantitative nature have been made. Even the commercially developed bacterial preparations known as Thuricide etc., have not been used extensively, except by highly trained professional entomologists. These preparations are effective against many lepidopteran pests when used according to the directions on the label, but for several reasons they have been used at only a nominal rate. One of the reasons is that they are slightly more expensive than most of the chemical poisons. There is a clear need for extension entomologists to recognize the usefulness of the bacterial preparations and promote their use more widely and forcefully. There seems to be a strong tendency for many extension entomologists to avoid recommending pesticides that do not carry a chemical name; thus, before pathogens are liable to be accepted, a re-education of entomologists will be necessary.

The efforts toward establishment of a clean environment will assist the development of better ecological utilization of natural controlling or regulating factors, including pathogens, in the management of insect pests. In this regard, we should be gathering appropriate ecological data of a long-term and predictive nature, at least on our present insect pests. Often bits of information are collected by several different investigators. Sometimes the motive for collecting the data is simply interest; and when interest wanes, the investigator may explore another, perhaps distantly related, facet. All the information gathered is potentially useful, but not necessarily essential for the solution of a practical problem. This is true for much entomological information. On the other hand, at least an equal amount of information is related directly to the short-term control or suppression of pest populations. A sustaining long-term approach has not been widely accepted as a realistic possibility; thus data have not been gathered to suit such an approach.

Classification and identification play an important primary role in the study of pathogens in insect populations, but there are so few workers involved in this area that an entomologist often can obtain only a very general name for a pathogenic or-

ganism. New micro-organisms associated with insects are being discovered at a relatively high rate, and with time we shall be able to provide more accurate identification. At present, a limited number of pathogens associated with a few pest species have been studied extensively enough to provide positive specific identifications. The actual naming of the micro-organism may not be as important as the understanding of its biology and ecology; therefore an entomologist or microbiologist should proceed with studies in these areas whether he has a name for the organism or not.

Simple numerical relationships (first-order relationships) should at least be examined. The incidence of the pathogen in the host species from one population to another (in space) and from one generation to another (in time) should be a primary consideration. This approach has already been used in the case of the European spruce sawfly, *Diprion hercyniae*, in North America where virus and parasite incidence data, collected regularly and systematically over a period of nearly 30 years, show that a nuclear-polyhedrosis virus exerts strong regulatory effects when host densities are high and that parasites are effective when host populations are relatively low (*Bird and Elgee 1957*; *Bird and Burk 1961*; *Neilson and Morris 1964*). The general sampling procedure used in the study of the European spruce sawfly can and should be used for the study of the numerical relationships of any micro-organism to its host.

Generally speaking, insects that die from disease and parasites fall to the ground, where they are difficult or nearly impossible to find, and soon decay. It is much easier and more accurate to collect a sample of living insects and place them in captivity for a period of time. During this time, with constant surveillance, all disease- and parasite-killed individuals can be detected, and the incidence of disease etc. for the time period can be estimated. From such incidence data, a series of samples in *time* and *space*, an accurate account of the interrelationships of the organisms can be constructed. This principle must be utilized more widely if we are to meet and solve pest problems on a sustaining scale, that is, without adversely affecting the general ecosystem for an extended time.

Incidence Differences

During the collection of such comprehensive incidence data, it is often discovered that a pathogen causes mortality only during certain stages in the life-cycle of the host (time), or that it has a high incidence in one population, but a low incidence in another (space) (*Harcourt 1966*). The reasons for these differences cannot necessarily be explained by the incidence data. For example, the relative susceptibility of individual hosts in a population may be highly variable, and certain stages may not be affected at all (*Stairs 1965*). Similarly, a population in one area may be composed of individuals that are generally more susceptible than those of a population occurring in another area (*Benz 1962*). To determine the ranges of host-susceptibility, experiments should be made under controlled conditions in the laboratory so that each individual can be observed more or less continuously. Once the general pattern and range of susceptibility are known, various field populations can be tested for specific differences by treating samples from these populations under controlled conditions in the laboratory.

An example to illustrate this procedure is the forest tent caterpillar, *Malacosoma disstria*-nuclear-polyhedrosis virus system. This pest insect species has been observed for nearly 100 years, and regular patterns of distribution and population fluctuations are evident. The species occurs over most of North America, but outbreak populations occur most frequently in the aspen stands that stretch across Canada and the northern United States. Many stands are stripped of early foliage for 5 to 8 years. During this time, parasites, predators, and diseases usually increase markedly and cause high mortality. In some stands, the major mortality factor may be parasites, while in others it may be virus. Often it appears that almost every larva in the population is infected with and killed by the virus. Following such decimation, the species may not be found in a stand for 8 or 10 years. This cycle of events is well documented and it suggests that the virus might be artificially disseminated for control of pest outbreaks (*Sippell 1962*).

In the early 1950's attempts were made to determine whether the virus could be applied to foliage to infect larvae feeding on

it, and thereby cause high mortality (*Bergold 1951*). Limited laboratory tests suggested that the larvae were relatively resistant to infection; thus only low mortality resulted. Therefore it was concluded that the virus would not be useful for artificial control of pest outbreaks. The questions of how the virus causes such massive mortality in natural populations were left unanswered. This presented a paradox. If it works in the field, why does it not work in the laboratory?

In the early 1960's some answers were obtained by a stepwise quantitative approach. Question one, what stages of the life cycle are susceptible to virus infection? The feeding larval stage, primarily. Question two, what is the relative susceptibility of young and old larvae? Many of the newly hatched larvae are susceptible to infection by a single virus unit, whereas many mature larvae are not susceptible to doses of a billion (10^9) virus units. Larval susceptibility decreases rapidly as the larvae grow older; thus the most effective time to disseminate the virus for population suppression is just as larvae hatch and begin to feed. Question three, what doses will cause high mortality? The food surface should be coated so that 100,000 (10^5) virus units are consumed by each young larva to ensure that 95 percent of the larvae will be killed (*Stairs 1965*). In actual field tests, concentrations of 10^7 polyhedra per ml. of water applied to thoroughly wet the foliage caused 92 percent larval mortality and prevented defoliation of the trees (*Stairs 1964*).

With answers to these three questions, we are able to predict the timing and quantity of virus that can be used for the successful suppression of pest populations, at least over small areas. The point of this discussion is that, when the problem was approached systematically by asking and answering the simplest and basic questions, a highly satisfactory result was obtained with a minimum of effort. This is, of course, a simplified example, but it illustrates that we do not necessarily need to obtain detailed information of a more complicated nature. It certainly illustrates that complicated theories can and do inhibit progress towards the utilization of pathogens for insect control.

Viral Latency

Simple quantitative relationships should be understood before theories concerning viral latency are proposed. There is little doubt that this theory has been detrimental to the progress of research and the development of viruses for practical use. All sudden virus epizootics can be explained on simple numerical terms. Even in forest tent caterpillar populations an epizootic can be initiated by a single polyhedron or virus unit.

A first-instar larva may be susceptible to infection by a single polyhedra. Such an individual will die in 4 to 8 days and will contain approximately 10^7 polyhedra. This is a 10 million-fold increase in virus incidence in the host population. It is enough virus to cause lethal infections of 8,000 second- and third-instar larvae, provided the virus reaches the food surfaces that will be consumed by these larvae. The gregarious feeding habits of the larvae insure that the virus from a single diseased larva dying among the group will almost certainly be contacted by some of the healthy larvae. These larger larvae will, in turn, become diseased, and each may contain as much as 10^{10} polyhedra at death in the fourth or fifth instar. This is 1,000 times as much virus as is contained in a first-instar larva. It is not enough, however, to infect more than 100 fourth- and fifth-instar larvae. These older larvae are about 10^8 times more resistant to infection than are first-instar larvae, and much greater quantities of virus must be present on the foliage before high mortality results.

Many larvae that are only lightly infected at the time of metamorphosis complete development to the adult stage. These adults (both sexes) transmit virus to their progeny, and foci of infectious virus are assured in the next generation of hosts. Epizootics often result from these foci and also probably from virus that survives on the plant surface and in the soil layers.

Recent studies on the persistence of virus in the soil suggests that considerable quantities may accumulate during an epizootic and remain infectious over long periods of time. The nuclear-polyhedrosis virus of *Trichoplusia ni*, the cabbage looper, will survive several years in the upper layers of the soil (*Jaques*

1967 a,b), and there is every reason to believe that other viruses of this group will survive in the soil or duff layers at least as long. Virus in the soil may be transmitted to the food plant, and hence to the host larvae, by anything that moves or causes the movement of soil particles to plant surfaces. Rain, wind, insects, birds, etc., are obvious agents of dissemination. Since an epizootic can be initiated by a single infectious polyhedron, it is quite possible that epizootics can develop in host populations from virus that remains in the soil during inter-outbreak periods. It is obvious that any detailed study of virus-host relationships should include infectivity studies of the soil.

Many of the foregoing comments will apply to any pathogenic organism. The same set of questions must be asked and answered before we can utilize an organism with any degree of precision and prediction. The distribution of the pathogen and host in time and space must be measured, and pathogen-host numerical interactions will then become obvious. In all cases, a pathogenic species is capable of existing apart from its host, at least for brief periods of time; thus simple spatial and temporal relationships are of basic importance to the survival of both species. These should be the first relationships investigated, and adherence to this simple principle will always yield valuable information.

Toxins

Several groups of pathogens are known to produce toxins specific for insects. Perhaps the best known are those produced by the *Bacillus* group of bacteria. The familiar *Bacillus thuringiensis* or Bt preparations owe their activity against insects largely to the presence of highly specific toxic substances. Of course, these make good "insecticides." The fungi also produce many kinds of toxins, and among those pathogenic for insects, species in the genera *Beauveria* and *Aspergillus* have been investigated. Although none has been exploited commercially, these toxins are good potential sources for insecticides.

It is generally believed by insect pathologists that large quantities of infectious pathogens must be available if the utilization

of the pathogens is to be successful. Thus much effort has been placed on the mass-production of these organisms. Only those of the *Bacillus* group have been developed on a functional, commercial scale; that is, one can purchase various formulations off the shelf from a farm chemicals distributor (*Briggs 1963*). These formulations are approved by appropriate public health agencies in most countries.

Several insect viruses have been tested, but none are being produced and marketed by commercial companies in the United States, pending approval of the U.S. Food and Drug Administration. Several companies are producing relatively large quantities of specific viruses so that, when proper licenses are obtained, these organisms will be immediately available for use. For example, the corn earworm and cotton bollworm nuclear polyhedrosis viruses (*Heliothis spp.*) are available at present but are licensed only for experimental use (*Ignoffo 1968*). The regulatory agencies in other countries have not been as strict; so in Canada, for example, viruses of sawflies are utilized by Christmas tree growers and foresters without control or interference by any government agencies.

Large quantities of the sawfly viruses are produced by confining susceptible larvae in cages and feeding them food contaminated with virus (*Bird 1953*; *Smirnoff et al. 1964*). After they have fed for 5 to 10 days, larvae become infected and begin to die. When the first larvae die, all are removed from the food and confined so that additional dead individuals can be collected easily. In the case of *Neodiprion sertifer*, an infested plantation of young Christmas trees can be sprayed with virus and large numbers of diseased larvae can be collected in a short time (*Bird 1964*).

Virus-diseased larvae are suspended in water, allowed to putrefy for several weeks or months and purified by differential centrifugation. A force 100 to 800 times gravity will sediment the polyhedra. The purity of the preparation depends upon the number and accuracy of the centrifugation. Often crude suspensions of recently diseased larvae are used without any particular treatment, and these have proved very effective. In cases where highly active and very pure preparations are required, the mid-

guts of diseased, but not yet dead, larvae are dissected out, washed, and placed in suspension. Since the virus multiplies only in the midgut cells, a maximum of virus and a minimum of uninfected tissue are obtained. This is probably the most efficient way of obtaining quantities of highly purified virus. If need be, the lumen of the midgut can be flushed to remove food particles and associated organisms before the midgut tissues are placed in suspension. These suspensions are among the purest obtainable.

The same principles may be used in the multiplication and production of the viruses of Lepidoptera. For the purest of preparations, diseased tissues may be dissected from sick individuals, macerated, and suspended in water or saline. If high purity is not required, the sick larvae may be allowed to die. They must be collected quickly, however, before they become liquified and difficult to handle. At this stage they readily disintegrate upon suspension in water, thus the virus is efficiently dispersed in the suspending medium. Often other microorganisms, especially bacteria, are present in such preparations, and it may be desirable to remove these, although they are not normally pathogenic. This may be done by using differential or zonal centrifugation techniques. Centrifuge techniques have much improved, and very pure, large quantity preparations can be obtained.

Host Larvae

Another problem in the production of large quantities of virus is the availability of a large number of host larvae. It is most convenient and least expensive to collect larvae from areas supporting high populations, bring them to the laboratory, infect them, and recover the virus (*Stairs 1964*). The recent development of artificial food media, however, has made possible the large-scale rearing of several pest species on a year-round basis in the laboratory (*Ignoffo 1968*). More progress will be made in this area in the immediate future, but even now several successful rearing programs are under way.

The infection of host larvae with virus is usually accomplished by contaminating the plant or food surface upon which

larvae are feeding. At high dosage levels a high proportion will usually succumb to virus disease. Occasionally the full-grown larvae are highly resistant to oral infection (*Stairs 1965*). For example, last-instar *M. disstria* larvae are very resistant; thus infection by feeding is very inefficient, so virus multiplication using this approach is not successful. To overcome this problem, virus particles, freed from polyhedra by pH treatment, were injected directly into the hemocoele. In this way, relatively low dosages caused very high disease mortality, and an extremely efficient method of virus multiplication was developed. Mature, fully fed larvae were collected from field populations, brought to the laboratory, injected with virus, and observed daily. Dead and dying individuals were removed and suspended in water. Often these suspensions were used immediately for dissemination into healthy host populations with good results. It was also found that storage in water at 4°C. in the dark for several months did not cause appreciable loss of viral activity.

The large-scale development of insect cell culture offers another method for the production of viruses and other obligate pathogens (*Grace 1962, 1966*; *Mitsuhashi 1966*; *Vaughn 1968*). However, many problems are associated with these artificial systems that must be solved before this approach can be employed successfully. For example, many cell lines are difficult to infect with viruses (*Vaughn and Faulkner 1963*).

Perhaps one of the most important factors in the successful utilization of a pathogen in the suppression of a pest population is insuring that enough of the pathogenic organisms reach the individual insects to cause lethal or debilitative infection. Certainly if the food plant (or other substrate) is thoroughly covered with a suspension (or dust cloud) of viable organisms, the chances of occurrence of infections are maximal. Water suspensions have proved to be satisfactory for small-scale tests, as have certain dust preparations (*Bird 1953*; *Thompson and Steinhaus 1950*). Emulsions have also been found to be effective (*Clark and Reiner 1956*; *Smirnoff et al. 1962*). Any sprayer that does not generate excessive heat may be used to disseminate pathogenic microorganisms. Aerosol space sprays and mist-blowers may be the most effective means of disseminating in-

sect pathogens. Much more quantitative investigation in this area must be done before maximum efficiency of dissemination is realized.

The integrated approach to pest control requires the manipulation of more than one factor of the pest's environment to cause a reduction in population and damage. Chemical control is based on the introduction of a poison into the insect's environment to cause mortality and population reduction. Similarly, parasites and predators have been introduced, usually one species at a time, to effect reductions in pest population levels. Very few attempts have been made to use a combination of chemicals, parasites, predators, and pathogens for the regulation of numbers of a pest species.

This approach is relatively complicated; and it requires, at least, that incidence data in space and time be obtained to determine the impact of each factor individually and collectively on the pest population levels. With these data in hand, relatively accurate predictions of population levels can be made, and the best manipulative procedures can be selected. In many cases, the artificial numerical increase of pathogens may be easiest and most effective over large areas. Local, small infested areas (fields or forest stands) may require careful treatment during a pest generation with a chemical to prevent excessive damage and great financial loss to an individual without causing undue disruption of the ecology over large areas. Similarly, local areas may be inundated with a pathogen, parasite, or predator. The result, however, may not be rapid enough to prevent damage and some financial loss. Modifications of these approaches are potentially useful in the management of many pest organisms, but they will be especially useful in the effective regulation of some of our major insect pests of forests.

References

Balch, R. E. and Bird, F. T.
1944. A DISEASE OF THE EUROPEAN SPRUCE SAWFLY, GILPINIA HERCYNIAE (HTG.), AND ITS PLACE IN NATURAL CONTROL. Sci. Agr. 25, 65-80.

Benz, G.
1962. UNTERSUCHUNGEN ÜBER DIE PATHOGENITÄT EINES GRANULOSIS VIRUS DES GRAUEN LÄRCHWICKLERS, ZEIRAPHERA DINIANA (GUÉNEÉ). Agronomski glasnik (Zagreb) 566-573.

Benz, G.
1964. ASPECTS OF VIRUS MULTIPLICATION AND AVERAGE REDUPLICATION TIME FOR A GRANULOSIS VIRUS OF ZEIRAPHERA DINIANA (GUENEE). Entomophaga Mem. 2: 418-421.

Bergold, G. H.
1951. NOTES ON POLYHEDRAL DISEASE OF FOREST TENT CATERPILLAR, MALACOSOMA DISSTRIA (HBN.). Can. Dep. Agr. Bimonthly Prog. Rep. 7(4): 1-2.

Bird, F. T.
1964. THE USE OF VIRUSES IN BIOLOGICAL CONTROL. Entomophaga Mem. 2: 465-473.

Bird, F. T.
1961. TRANSMISSION OF SOME INSECT VIRUSES WITH PARTICULAR REFERENCE TO OVARIAL TRANSMISSION AND ITS IMPORTANCE IN THE DEVELOPMENT OF EPIZOOTICS J. Insect Pathol. 3: 352-380.

Bird, F. T. and Elgee, D. E.
1957. VIRUS DISEASES AND INTRODUCED PARASITES AS FACTORS CONTROLLING THE EUROPEAN SPRUCE SAWFLY, DIPRON HERCYNIAE (HTG.) IN CENTRAL NEW BRUNSWICK. Can. Entomol. 89: 371-378.

Bird, F. T. and Burk, J. M.
1961. ARTIFICIALLY DISSEMINATED VIRUS AS A FACTOR CONTROLLING THE EUROPEAN SPRUCE SAWFLY, DIPRION HERCYNIAE (HTG.), IN THE ABSENCE OF INTRODUCED PARASITES. Can. Entomol. 93: 228-238.

Briggs, J. D.
1963. COMMERCIAL PRODUCTION OF INSECT PATHOGENS. IN INSECT PATHOLOGY, AN ADVANCED TREATISE. E. A. Steinhaus Ed. Vol. 2: 519-548.

Bucher, G. E.
1958. GENERAL SUMMARY AND REVIEW OF UTILIZATION OF DISEASE TO CONTROL INSECTS. 10th Int. Congr. Entomol. Proc. (1956), 4: 695-701 Montreal.

Clark, E. C. and Reiner, C. E.
1956. THE POSSIBLE USE OF A POLYHEDROSIS VIRUS IN THE CONTROL OF THE GREAT BASIN CATERPILLAR. J. Econ. Entomol. 49: 653-659.

Dutky, S. E.
1959. INSECT MICROBIOLOGY. Adv. Appl. Microbiol. 1: 175-200.

Grace, T. D. C.
1962. ESTABLISHMENT OF FOUR STRAINS OF CELLS FROM INSECT TISSUES GROWN IN VITRO. Nature 195: 788-789. London.

Grace, T. D. C.
1966. ESTABLISHMENT OF A LINE OF MOSQUITO (AEDES AEGYPTI L.) CELLS GROWN IN VITRO. Nature 211: 366-367. London.

Harcourt, D. G.
1966. MAJOR FACTORS IN SURVIVAL OF THE IMMATURE STAGES OF PIERIS RAPAE (L.). Can. Entomol. 98: 653-662.

Heimpel, A. M. and Angus, T. A.
1960. BACTERIAL INSECTICIDES. Bacteriol. Rev. 24: 266-288.

Ignoffo, C. M.
1968. VIRUSES- LIVING INSECTICIDES. CURRENT TOPICS IN MICROBIOLOGY 42: 129-167.

Jacques, R. P.
1967a. THE PERSISTANCE OF A NUCLEAR POLYHEDROSIS VIRUS IN THE HABITAT OF THE HOST INSECT, TRICHOPLUSIA NI. I. Polyhedra deposited on foliage. Can. Entomol. 99: 785-794.

Jacques, R. P.
1967b. THE PERSISTANCE OF A NUCLEAR POLYHEDROSIS VIRUS IN THE HABITAT OF THE HOST INSECT, TRICHOPLUSIA NI. II. Polyhedra in soil. Can. Entomol. 99: 820-829.

Mitsuhashi, J.
1966. TISSUE CULTURE OF THE RICE STEM BORER, CHILO SUPPRESSALIS WALKER (LEPIDOPTERA, PYRALIDAE). II. MORPHOLOGY AND IN VITRO CULTIVATION OF HEMOCYTES. Appl. Entomol. Zool. 1: 5-20.

Neilson, M. M. and Morris, R. F.
1964. THE REGULATION OF EUROPEAN

SPRUCE SAWFLY NUMBERS IN THE MARITIME PROVINCES OF CANADA FROM 1937 TO 1963. Can. Entomol. 96: 773-784.

Sippell, W. L.
1962. OUTBREAKS OF THE FOREST TENT CATERPILLARS, MALACOSOMA DISSTRIA HBN., A PERIODIC DEFOLIATOR OF BROAD-LEAVED TREES IN ONTARIO. Can. Entomol. 94:4, 408.

Smirnoff, W. A., Fettis, J. J. and Haliburton, W.
1962. A VIRUS DISEASE OF SWAINE'S JACK PINE SAWFLY, *NEODIPRION* SWAINEI, MIDD. SPRAYED FROM AN AIRCRAFT. Can. Entomol. 94: 477-486.

Stairs, G. R.
1964. DISSEMINATION OF NUCLEAR-POLYHEDROSIS VIRUS AGAINST THE FOREST TENT CATERPILLAR, MALACOSOMA DISSTRIA (HUBNER) (LEPIDOPTERA: LASIOCAMPIDAE). Can. Entomol. 96: 1017-1020.

Stairs, G. R.
1965. QUANTITATIVE DIFFERENCES IN SUSCEPTIBILITY TO NUCLEAR-POLYHEDROSIS VIRUS AMONG LARVAL INSTARS OF THE FOREST TENT CATERPILLAR, MALACOSOMA DISSTRIA (HUBNER). J. Invert. Pathol. 7: 427-429.

Steinhaus, E. A. 1949. PRINCIPLES OF INSECT PATHOLOGY: 757 pp. McGraw-Hill, New York.

Thompson, C. G. and Steinhaus, E. A.
1950. FURTHER TESTS USING A POLYHEDROSIS VIRUS TO CONTROL THE ALFALFA CATERPILLAR. Hilgardia 19: 411-445.

Vaughn, J. L.
1968. A REVIEW OF THE USE OF INSECT TISSUE CULTURE FOR THE STUDY OF INSECT ASSOCIATED VIRUSES. Current topics in microbiology 42: 108-128.

Vaughn, J. L. and Faulkner, P.
1963. SUSCEPTIBILITY OF AN INSECT TISSUE CULTURE TO INFECTION BY VIRUS PREPARATIONS OF THE NUCLEAR-POLYHEDROSIS VIRUS OF THE SILKWORM. (Bombyx mori L). Virology 20: 484-489.

■

PARASITES

by W. J. TURNOCK, Science Secretariat, Ottawa, Ontario; and J. A. MULDREW, Canadian Forestry Service, Edmonton, Alberta.

INTEGRATED CONTROL signifies the selection and use of various methods of applied control to harmonize with the natural control factors already operating. It cannot be applied until the roles and relative importance of these natural control factors are known. The prerequisites to its use are a knowledge of both basic ecological principles and the ecological features that are specific to each target species. The goal is to achieve the minimum degree of damage to the product that is consistent with both minimum damage to the environment due to side effects of control measures and maximum long-term economy. These side effects, primarily due to insecticides, are now well known: (1) development of resistance, (2) resurgence of treated populations, (3) outbreaks of secondary pests, (4) contamination of the environment by persistent poisons, and (5) destruction of beneficial species.

Objectives of Biological Control Programs

In the past, the degree to which a biological-control operation has been considered successful has been judged on the extent to which the introduced agents have provided the ultimate in control—the permanent maintenance of a pest's abundance below the level of economic injury. For example, DeBach (*1964*) differentiates between outstanding success, substantial success, and partial success. The assessment of a particular case is made on the basis of: (1) the proportion of the total range of the pest in which control is achieved, (2) the degree to which the duration or severity of outbreaks is reduced or the duration of the

intervals between outbreaks is increased; (3) whether supplementary control methods must be used, and (4) whether a pest is of great or slight economic importance.

It has been suggested, for example by Prebble (*1960*), that with certain types of pests where only very high densities cause appreciable damage, a program might be deemed fully successful if the degree of economic injury is significantly reduced even though less severe and less prolonged outbreaks still occur.

The biological-control program against the gypsy moth can be cited as an example where the evaluation of degree of success would depend on what the original objective of the program was considered to be. DeBach (*1964*) rated it as a "partial success" even though Clausen (*1956*) said that the end result in America was that outbreaks were reduced to a level "comparable in range and severity" to those occurring in Europe. If this degree of control had been set originally as a realistic objective, then the final rating might have been a substantial or even an outstanding success. In this program the effectiveness of the introduced agents has undoubtedly been inhibited by the continuing and widespread use of insecticides against the pest.

Although biological-control specialists have long recognized the importance of partial control, some of the early spectacular and complete successes have encouraged the setting of impossibly high standards for judging the usefulness of biological-control attempts. Such standards discourage attempts aimed toward partial control, which could reduce the frequency, severity, or duration of damage. Prebble (*1960*) criticized this all-or-none attitude toward control operations as being incompatible with our increasing knowledge of population dynamics and forest ecosystems; but the attitude still persists.

Philosophy Underlying Biological Control

Biological-control workers have stressed the importance of governing factors in the total complex that restricts population increase. Governing factors are defined as those that are affected by changes in population density and, as a result, modify their influence so as to oppose population change (*Nicholson 1954*). However, many factors to which the above definition of

governing can be applied, are restricted in their ability to influence population change. These factors may have a limited ability to respond to large increases in density and operate only in endemic populations. Certain parasites of spruce budworm (*Miller 1963*) and elaterid predators of the pine looper (*Turnock 1969*) are examples. Other factors such as diseases may operate only at high densities.

The relative importance of parasites that are effective at low host densities versus those capable of reducing outbreak populations is one that cannot be answered on the basis of available information on population dynamics. The most effective parasite species would be capable of operating effectively both at low host densities and under outbreak conditions. Certainly some parasites that are capable of terminating an outbreak are also effective at low densities: *Cyzenis albicans* and *Agropyron flaveolatum* on the winter moth in Nova Scotia (*Embree 1965*); *Agathis pumila* and *Chrysocharis laricinellae* on the larch casebearer in eastern-central North America; *Olesicampe benefactor* on low larch sawfly populations in alpine Europe and outbreak populations in Manitoba. On the other hand, the collapse of the original European spruce sawfly outbreak in North America was caused by an introduced virus, while subsequent outbreaks have been controlled by the combined influence of the virus and two parasite species, or, in some cases, either virus or parasites acting alone. The parasites are particularly effective at very low host densities and are sensitive to minor fluctuations at these levels (*Neilson et al., in press*).

We suggest that, wherever a particular biotic agent has the capability of maintaining population levels permanently within given limits of abundance that are non-damaging, the qualifying word "effective" be used to describe it. Such agents are effective as long as the non-governing mortality factors show no marked deviations from their long-term average influence.

It seems probable there may be situations in which a complex of governing factors, none of which by itself is an "effective governing agent," act together in such a way as to be effective. The possibility of "stacking" a number of partially governing agents to attain effective control requires more study. A basic

cleavage of opinion exists as to whether or not a single introduction of the best possible parasite species is preferable to multiple introductions. Though while the introduction of competing species may be detrimental to the more efficient of the two, i.e., the case of *Eulimneria rufifemur* interfering with *Orgilus obscurator* attacking the European pine shoot moth (*Pschorn-Walcher et al. 1969, Syme in press*), such examples cannot be automatically extended to reach the conclusion that a single parasite species will be more effective than several species.

Non-governing factors such as weather may be necessary components of processes that are density-dependent in action. For example, when the average degree of protection afforded by living places decreases as population density increases, percentage mortality due to adverse weather also increases. Similarly, crowding phenomena may render individuals more susceptible to adverse weather by changing their behavioral and/or physiological characteristics.

Insecticidal applications usually correspond in their effect to the catastrophic mortalities that occur when weather conditions are severe. Since they are normally applied only at very high densities of the pest, they are density-dependent to a degree. Their application, however, may elicit the sort of homeostatic mechanisms that force the pest to remain at high densities most of the time (*National Academy of Sciences 1969*). The spruce budworm outbreak in south-central New Brunswick apparently illustrates this situation: since 1960, an average of over 1,600,000 acres has been sprayed annually to minimize tree mortality. Although this objective has been attained, the outbreak continues and surveys indicate that 10 million acres will be defoliated in 1970 (70 percent of them will have moderate to severe defoliation) and plans are under way to spray about 3 million acres.

It should be possible to use insecticides in a density-governing way by interposing man as the controlling component to create a feedback loop. In such a case the application of insecticides would be varied in time, space, and intensity to stabilize population levels rather than to produce high mortalities. Man

may also be able to achieve such results by regulating microclimates; for example, the humidity in tree nurseries or plantings could be modified to vary the intensity of mortality due to disease. Other control methods that could be utilized in a governing way through human intervention are: the use of antifeedants, repellents, pheromones, chemosterilants, radiation sterilization, electromagnetic energy, and behavioral or genetic manipulation.

It has been implied above that the reason most pest species are pests is because there are no effective governing processes acting against them. Even with pest species, however, certain governing processes eventually come into play if density continues to increase, namely those connected with food shortage, or reduced fecundity or viability. Below such density levels it is likely that non-governing processes connected with weather, food quality, etc. are major determinants of annual changes in population level.

Among the reactive factors it is parasites, invertebrate predators, and diseases that are considered to have a special potential for governing populations. Although their functional responses and "behavioral numerical responses" (*sensu Buckner 1966*) may be of considerable importance, particularly at lower levels of host density, their most important characteristic is that their "breeding numerical response" (*sensu Buckner 1966*) is potentially limited only by host density and is not restricted by factors such as territorial behavior.

The breeding numerical response of a particular species is probably at least partly dependent on its functional response (i.e., if there is an increase in the number of hosts attacked per parasite with an increase in host density, this results in an increase in the ratio of adult parasites to adult hosts in the next generation). In order for the agent to exert a governing action, the total response during one or more generations to an increase in host populations must result in a sufficiently large increase in mortality to cause a reversal of the population trend. The behavioral numerical response of avian predators to concentrations of insect prey certainly increases prey mortality (*Buckner and Turnock 1965; Mattson et al. 1968*), but its effec-

tiveness as a governing factor is not well documented.

In the control of the Klamath weed by *Chrysolina quadrigemina* in California and the prickly pear cactus by *Cactoblastus cactorum*, the phenomenon of local annihilation of both host and agent has occurred. This has been followed by re-invasion; first by the host and later, sometimes after an interval of sufficient duration to allow the host to build up appreciably, by the agent. Huffaker and Messenger (*1964*) state that following re-invasion of the Klamath weed, a great variety of forces (rainfall, temperature, fire, etc.) may devastate or destroy these stands in the absence of the beetle. A population-dynamics study in such stands during this period would show that physical factors would be of major importance in determining annual changes in population levels. They state, however, that the beetle still holds the key role since whenever stand densities become threateningly high the beetle invariably arrives by dispersal from residual populations elsewhere and drastically reduces or annihilates these populations. The true role of the beetle could be determined only by a long-term population-dynamics study.

It is not known how important local annihilation and resulting fragmentation of host populations is when insect pests are controlled by biotic agents, but it is obviously worthy of considerable study. Wolcott (*1958*) cites two examples where biological control of pests in Puerto Rico was too successful, resulting in the disappearance of the agents from the island and the later reappearance of the pests, but not the agents. In continental areas the phenomenon may be of relatively common occurrence, particularly with hosts against which biological control has been successful; but if the local annihilation occurs over a comparatively small area and is of relatively short duration, it would be difficult to detect. Andrewartha and Birch (*1954*) believe it is going on around us all the time, although due to underpopulation phenomena rather than to excessive kill by biotic agents, whereas Varley and Gradwell (*1970*) believe it is not common in the field.

At the borders of distribution of some species, environmental pressure may be so severe that only temporary existence is pos-

sible, and it is usually only in the more optimal areas that a pest species periodically increases to excessive numbers. In the intermediate areas the species may be a relatively permanent occupant, but its numbers rarely rise to injurious levels. In these areas it probably becomes extinct periodically, and populations are re-established by immigration from the optimum zone. If the only effective governing processes in the optimum zone are those connected with depletion of the food supply, we should not expect to find other governing processes in the intermediate areas where, because of the lower densities of host, there is no competition for food. A possible example of such a species is *Bupalus piniarius*, which is a serious pest in Germany, England, etc., where it is limited mainly by food depletion. A thorough population-dynamics study of low-density populations in Holland (*Klomp 1966*) failed to reveal the presence of an effective governing homeostatic mechanism.

It has long been postulated (*Nicholson and Bailey 1935*) that a delay or lag in the response of a parasite or predator to an increase in host density gives rise to coupled oscillations of host and agent that increase in amplitude with time and are inevitably self-destructive. Varley and Gradwell (*1970*) state that only specific and synchronized enemies act in this way. This would suggest that such specific enemies would not be effective biological control agents. Support for this view is given by the conclusion of Liu Chung-lo (*1962*) whose analysis of 30 successful attempts indicated that moderate polyphagy will better ensure success than monophagy. On the other hand, Doutt and DeBach (*1964*) conclude that most successes in biological control have resulted from the introduction of rather host-specific entomophagous species having good synchronization.

Klomp (*1966*) states that oscillations of increasing amplitude are never observed under natural conditions because they would lead to extinction. However, such oscillations might occur in nature under unusual circumstances such as the introduction of a specific, well-synchronized parasite. This may have occurred in Puerto Rico, where the extinction of two entomophagous species was observed. The lack of observations of this phenomenon may be related to its ephemeral nature: either the system is

stabilized or extinction occurs rapidly.

Coupled oscillations of increasing amplitude can be stabilized into coupled oscillations of approximately constant amplitude by damping mechanisms. As a generality, a damping mechanism can be any interference component that reduces the efficiency of enemies as prey density increases. Varley and Gradwell (*1970*) concluded from a study of models that it is impossible to mimic the coexistence of two specific parasites unless each is provided with its own density-dependent mortality. Huffaker and Kennett (*1969*) present data indicating that the effective area of discovery (searching capacity) of the ichneumonid *Venturia canescens* decreases as host density increases, and this would tend to dampen oscillations because the parasite is acting as its own density dependent factor.

Do the results of population-dynamics studies lend support to the above views? Studies on defoliators that occasionally reach very damaging densities, such as the spruce budworm (*Morris 1963*), the lodgepole needle miner (*Stark 1959*), and the larch sawfly (*Ives et al. 1968*), indicate that the determination of density levels below those causing food shortage is usually due to climatic causes or non-governing biotic agents. There are certain biotic agents that seem to become abundant only after very high densities are reached; and although these may play an important role in decreasing the duration of outbreaks, they are not effective in terms of governing—i.e., preventing the excessive increases in host density in the first place.

Some species that have been studied intensively have been shown to have their densities at all levels determined mainly by parasites. One of these is the black-headed budworm in the Maritimes (*Morris 1959*; *Miller 1966*) which, in this region, occasionally reaches high densities for short periods. Miller concluded that population release was associated with years of low parasitism and favorable weather, while population decline was associated with late larval parasitism. This defoliator has caused mortality of western hemlock on the West Coast, and a population analysis in this area might show a basic difference in the population-level determinants as compared to the Maritimes. Varley and Gradwell (*1970*) caution that in Morris's analysis,

parasitism is causally responsible for rather less than half of the population change, even though estimations of parasitism in year N allow a reasonable prediction of population density in year N+1. This is because the residual mortality varies in a way similar to variations in larval parasitism, and these authors believe that the unstudied aspects such as parasites or predators acting in the egg or pupal stages contain a major cause of host density fluctuations. They believe an identical situation occurs in the case of the grey larch moth (*Zeiraphera diniana Gn*). Concerning this latter species, however, Auer (*1969*) concluded, from an analysis using a five-factor model, that, within the optimal area, "The biological and density-dependent actions are much more efficient than the abiotical actions." Preliminary results of a study of the fall webworm (*Morris 1969*) indicate that American populations are maintained at a low level mainly by the effects of heat accumulation on survival. However, he suggests that simulation studies using a biologically meaningful model, now in preparation, will be necessary to determine the role of density dependence in the webworm's system of regulation.

The results of these studies give conflicting answers to the question of whether effective governing factors maintain the low densities of non-pests. Many studies have documented the absence of effective governing factors during epidemics of pestiferous species which, at such times, can be aptly described as out of control. There have been too few attempts to identify the presence of such factors in species that have never been pestiferous. Comparative studies of population regulation of pests under both endemic and epidemic conditions are necessary for the development of rational pest management.

Classification of Pestiferous Species

The "classical" approach to biological control was initially developed when it was realized that exotic pests commonly lacked the natural agents that prevented their depredations in their place of origin. Unfortunately, however, the idea that biological control consisted solely of the introduction of enemies from foreign lands has tended to dominate discussions of the

potential of biological control (*e.g., Simmond's 1956 critique of Taylor 1955*) to the detriment of consideration of alternate approaches and emphasis on the need to fit the approach to the characteristics of the target species.

There are different types of pests that vary in their suspectibility to the classical approach, and in this paper we recognize four categories of pest insects that differ in their origin, the mechanisms that determine their population levels, or the relative densities at which damage occurs.

1. *Exotic pests:* species originating from other regions, which lack the effective governing mechanisms that are present in their native habitat.

2. *Anthropogenic pests:* species whose populations reach damaging levels due to changes made in the environment by man's activities.

3. *Opportunistic pests:* species with a "wide-amplitude" type of population behavior (*Watt 1968*), which periodically reach very high densities in response to favorable environmental conditions.

4. *Low-density pests:* species that occur at low densities, apparently due to the action of effective governing mechanisms, but nevertheless cause economic damage.

Exotic pests have traditionally been considered the most promising targets for biological-control operations because, in their native habitat, they occur at non-economic densities, presumably due to effective governing mechanisms. Living biotic agents are important components of governing mechanisms, and these agents often can be transported and established in the invaded region.

Anthropogenic pests resemble exotic pests in that they are effectively governed in some areas, but differ in that they are not effectively governed in habitats that have been greatly modified by human activity. Since effective biotic agents usually exist in adjacent undisturbed areas, these modifications appear to have created an environment that limits the effectiveness of these agents. Biological control through colonization is therefore un-

likely to be successful unless (1) the environment is changed to ameliorate the limiting factors or (2) biotic agents adapted to the modified environment are discovered or developed.

Opportunistic pests are characterized by extraordinarily wide-amplitude population fluctuations wherever conditions of food and weather are favorable. Their great reproductive potential and great powers of dispersal resemble those of the opportunistic species described by Cole (*1966*): "plants and animals that are normally inconspicuous but that quickly invade and occupy a temporary habitat." These pests may be attacked by a large complex of biotic agents, but are regarded as being largely under the influence of density-independent rather than density-dependent factors (*Watt 1968*).

The lack of sources of new biotic agents attacking pests of this type has discouraged the biological control approach, and the few attempts made have failed (i.e., the spruce budworm; *Miller and Angus, in press*). Although these species are frequently abundant over wide areas in their native lands, it is remarkable that few of them have become pests in other continents. This apparent inability to colonize new areas may be related to the importance of density-independent factors in their life systems. The same non-governing factors that determine generation survival in the native land are likely to be present and of similar importance in the new environment. The chance of such a species becoming established in a new region might therefore only be high during the relatively brief periods when these factors are favourable. On the other hand, species whose fluctuations are determined by biotic governing factors, except competition for food, escape these governing influences in a new environment and commonly find combinations of density-independent factors that are suitable for both establishment and rapid increase.

Thus a species exhibiting low-amplitude population fluctuations in its native home would probably be characterized by wide-amplitude fluctuations in a new environment, possibly exceeding those characteristic of native opportunistic pests. Such species in a new environment may continue to increase until the food supply is almost totally destroyed, thus leading to their

own extinction in localized areas and marked instability of the ecosystem of which they form a part.

Low-density pests present a difficult problem for biological control. They do not exhibit wide-amplitude population fluctuations and are usually considered to be well governed. Since effective density-dependent agents are already present, there is not much scope for classical biological-control approaches. This category includes many of the species called "direct pests" by Turnbull and Chant (*1961*) but excludes those direct pests that attain high densities. Although classification on the basis of direct or indirect damage is useful for emphasizing the degree of population reduction necessary for economic control, classification on the basis of the population dynamics of the pest gives a more realistic evaluation of the best strategy for an integrated control program. For example, *Adelges piceae* is a species that is classified as a "direct pest" by Turnbull and Chant (*1961*). We would classify it as typically anthropogenic in Europe, where it is endemic on the older trees of the common silver fir *Abies alba* in mature stands but often a pest in the mixed age plantings that have been made outside the natural range (*Pschorn-Walcher 1964*), and as typically exotic in America.

The development of integrated control strategies must be based on both the population characteristics of the pest and the various types of control operation that are available. Past experience, theory, and investigation of specific situations should dictate the most promising integrated control approach. A large proportion of past biological-control programs have utilized parasites; and this experience, plus the theory developed from population-dynamics studies, provides a basis for utilizing parasites in integrated control programs.

Analysis of Programs Against Forest Insects

The history of biological-control attempts against forest insects in North America has been reviewed by Dowden (*1962*) and McGugan and Coppel (*1962*). They list 44 target species for programs in which parasites were used; and we added a 45th species, the holly leaf miner, following Turnbull and Chant

(*1961*). Since the period covered by these reviews, a few new programs involving parasites have been initiated: against the larch sawfly, the European pine shoot moth, the European pine sawfly, and the winter moth in Canada; and against the European elm bark beetle, the larch casebearer, and the western spruce budworm in the U.S.A.

The record of parasite releases against forest pests is rather blurred and confused in places. In attempting to evaluate this record, we have been forced to make decisions regarding the various programs on the basis of incomplete data. The results may be biased, but, if we are to advocate the use of parasites in integrated control programs, we must be prepared to give some estimate of the chances of success.

On the basis of published information, each target species was classified as to pest type (exotic, anthropogenic, opportunistic, low-density) and whether it was a "prime" or "alternative" target for parasite releases: prime targets are known to be hosts of the parasite species released against them; alternative targets are those against which parasites from related host species were released on the basis of a reasonable chance of success or merely to dispose of surplus material. In this empirical evaluation it was necessary to exclude a large number of the programs listed because: release and recovery data were inadequate; the parasite was probably already present; only a single release of the parasite was made; the parasite was introduced to Canada from a subtropical source; the parasites released were obtained from host species distantly related and ecologically dissimilar from the target species.

Most of the 21 programs that were considered amenable to analysis, and most of the successful programs, were against exotic pests (table 1). Only three attempts were made against anthropogenic and two against opportunistic pests. Among these five, the single successful biological control attempt was against an anthropogenic pest, the pine tip moth, and in this case the pest situation had many resemblances to that of an exotic pest: serious damage to pine plantations was being caused by *Rhyacionia frustrana bushnelli* in Nebraska where effective parasites were absent; while *R. frustrana frustrana* in Virginia was effec-

Table 1—Target Species for Major Biological Control Programs Using Parasites Against Forest Insects in North America

Species	Origin	Type[1]	Results[2]
HOMOPTERA			
Lecanium tiliae L.—lecanium scale	Exotic	Prime	C
Gossyparia spuria (Mod.)—European elm scale	"	"	S
COLEOPTERA			
Galerucella xanthomelaena (Schr.)—elm leaf beetle	"	"	C
DIPTERA			
Phytomyza ilicis (Curt.)—Holly leaf miner	"	"	C
LEPIDOPTERA			
Choristoneura fumiferana (Clem.)—spruce budworm	Native	"	U
Cnidocampa flavescens (Wlkr.)—oriental moth	Exotic	"	C
Coleophora laricella (Hbn.)—larch casebearer	"	"	S
Hemerocampa leucostigma (J. E. Smith)—white-marked tussock moth	Native	Alternative	U
Lambdina fiscellaria (Guen.)—eastern hemlock looper	"	Prime	U
Operophthera brumata (L.)—winter moth	Exotic	"	S
Porthetria dispar (L.)—gypsy moth	"	"	C
Nygmia phaerrhoea (Donov.)—brown-tail moth	"	"	C
Rhyacionia frustrana bushnelli (Busck)—pine tip moth	Native	"	S
Rhyacionia buoliana (Schiff.)—European pine shoot moth	Exotic	Prime	U
Stilpnotia salicis (L.)—satin moth	"	"	C
HYMENOPTERA			
Diprion hercyniae (Htg.)—European spruce sawfly	"	"	S
Diprion similis (Htg.)—introduced pine sawfly	"	"	S
Heterarthrus nemoratus (Fall.)—birch leaf-mining sawfly	"	"	C

Neodiprion lecontei (Fitch)—red-headed pine sawfly	Native	Alternative	U
Neodiprion sertifer (Geoff.)—European pine sawfly	Exotic	Prime	U
Pristiphora erichsonii (Htg.)—larch sawfly	" [3]	"	C

[1]See text for definitions.
[2]U = Unsuccessful, C = Contributive, S = Successful—See text for definitions.
[3]Origin disputed but here listed as "Exotic" because of its poor complex of parasites in North America (*Pschorn-Walcher 1963*).

tively controlled by parasites (*Dowden 1962*). The distribution of the two subspecies was disjunct, and thus this example cannot be used to predict the results of parasite releases against anthropogenic pests.

Consideration of the results of parasite releases against native (anthropogenic plus opportunistic) and exotic pests suggests that prospects for manipulating pest populations with pest releases are quite good (table 2). At least one new parasite was established on all the exotic species and on 40 percent of the native target species. The lesser success of releases against native target species may be taken to indicate that these pests are less suitable to the establishment of new parasites, but the record also suggests that the effort applied to these programs has been less than for introduced pests: the average number of parasite species released per native pest is 7.8; per exotic pest it is 9.4.

The results indicate that the prospect for quantitatively increasing the parasite complex is high for exotic pests and reasonably good for native pests. The fortuitous establishment of parasites released against the gypsy and browntail moths, the European spruce sawfly, and the European pine sawfly also shows that the parasite complex of native species can be increased by introductions.

The rate of successful establishment in relation to the total number of parasite species released was approximately one-third (table 2). This is undoubtedly a gross underestimate of the probability that an introduced species can be established, because in many programs difficulties with handling, synchroniza-

Table 2.—Results of Biological Control Programs Using Parasites Against Forest Insects in North America

Origin of target species	Type of program[1]	Number of species		Establishment (%)—		Control[1] (% of target species)			Excluded species
		Target	Parasites released	on target spp.[2]	of parasite spp.[3]	C	S	C + S	
		No.	*No.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*Pct.*	*No.*
Native	Prime	3	28	33	4	0	33	33	2
	Alternative	2	11	50	18	0	0	0	17
Exotic	Prime	16	151	100	37	56	31	88	2
	Alternative	0							3
All species	—	21	190	90	32	43	29	71	24

[1]See text for definitions.
[2]Target species on which at least one new parasite was established/total target species.
[3]Number of parasite species established/total number of species released.

tion, and small numbers of parasites available, mitigated against success. In our own experience, the failure of four of the six species of parasites released against the larch sawfly since 1961 can be attributed mainly to our lack of knowledge of conditions necessary to ensure mating and maintain vigor of parasite adults between emergence and release (*Turnock and Muldrew, in press*).

Evaluation of the effect of the introduction of a parasite on the target species should be based not only on its contribution to a reduction in pest population levels, but also to the reduction in damage to trees. Unfortunately, such information is rarely collected, and for many programs even crude data on the level of parasitism in the population is available for only a few years following the release. We therefore evaluate the biological-control programs on the basis of three categories:

1. *Successful:* populations and damage reduced to acceptable levels.
2. *Contributive:* introduced parasites causing appreciable mortality and believed to be contributing to the reduction of the intensity, duration, or frequency of outbreaks of the target species.
3. *Unsuccessful:* released parasites either not recovered, or occurring sporadically or at very low numbers.

Successful control was attained against 31 percent of the exotic and 33 percent of the native pests that were prime targets for parasite introduction. Contributive control was attained against 56 percent of the exotics but none of the native pests. The latter group comprises too small a number of species to allow the conclusion that parasite introductions are unlikely to contribute to the control of native pests.

Evaluation of Past Programs

Parasite release has been shown to have had some controlling effect on pest populations in a remarkably high proportion of the attempts, even though cases have been included where the

knowledge and resources applied to the program were minimal. The failure to adequately support biological-control programs can in part be attributed to the prevalence of too casual an attitude to the problems of parasite establishment. Although we eliminated from consideration many ill-conceived or poorly executed programs, the remainder still includes cases where parasites were released in poor condition, in poor synchronization with the preferred host stage, unmated, in inadequate numbers, or in suboptimal environments.

The problems of past programs can be attributed basically to a lack of proper standards in scientific procedure. Too often, little attention has been paid to researching the problems, to selecting appropriate biotic agents, to ensuring proper care of these agents before release, to selecting optimum release areas, and to assessing the host-density determinants before and after the initiation of the program. Reasons for this have been that many programs were conducted by forest entomologists lacking an adequate background in population dynamics and biological control and that financial support has been inadequate. Past expenditures on biological control have been small in relation to both the benefits achieved and the expenditures made on chemical control. The favorable cost-benefit ratio of biological control would be even more impressive if the costs due to undesirable side-effects of chemical control and possible future detoxification of polluted environments could be included. At present there is too little appreciation of the relatively low cost and lasting benefits of biological control. Since there is slight incentive for industry to develop biological control, public bodies must accept the responsibility for encouraging and supporting this type of program.

Recommendations for Parasite Use in Integrated Control

Integrated control for forest pests is applied population dynamics (*Balch 1964*). Continued maintenance of pest numbers below the economic threshold for damage must be based on knowledge of pest ecology and damage thresholds. In selecting

control methods for use in integrated programs, an attempt should be made to forecast the effects of specific actions on other mortality factors and short- and long-term population trends. In the absence of good models for predicting population trends, integrated control planning should initially concentrate on the evaluation of existing natural control. In analyses of the target species, the efficiency of natural and applied control factors and their inter-actions must be examined for different stages of the insect and for different ecological situations in which the pest occurs.

The concept of "guilds" of biological agents attacking a pest appears to be a very useful tool in planning integrated control. Root (*1967*) defines a guild as "a group of species that exploit the same class of environmental resources in the same way. This term groups together species, without regard to taxonomic position, that overlap significantly in their niche requirements." This can be considered as an expansion of the concept of "parasitological niches" defined by Zwolfer (*1961*) in the following way: ". . . holometabolic insects (possess) several biologically and ecologically differentiated stages, which are attacked by a number of different types of parasites. Host species such as these offer to entomophagous insects a system of diversified opportunities for oviposition and larval development, providing what, in analogy with the ecological niches of the habitat, may be considered as a complex of parasitological niches."

Although this concept is useful in investigating the parasite complex of pest species to reveal niches where the parasite complex is deficient in species or in effectiveness, the "guild" concept has a wider application. The target species can be considered as offering a complex of niches, which are exploited, to a greater or lesser degree, by the various guilds of biological agents. These guilds may attack different life stages of the pest, or individuals that occur in particular parts of trees, stand types, or site conditions. For example, for certain pests it may be sufficient to determine that the guild of larval parasites, predators, and diseases is lacking in species and effectiveness, while for other species the larval guild may be efficient in some stands and climatic zones but not in others. Thus in west-

ern larch stands the larch sawfly larval parasite guild appears reasonably effective (*Molnar et al. 1966*) while the same guild is ineffective in continental stands of tamarack, apparently because the "resistant" strain of larch sawfly is present (*Muldrew 1953*), as well as in tamarack stands of Newfoundland, possibly because of unfavorable climatic conditions. The approaches to integrated control in these three situations would be quite different.

Utilization of parasites in control operations can involve various methods of releasing parasites, of enhancing parasite efficiency by manipulating other aspects of the environment, and of using parasites to improve other mortality factors. Most parasite releases against forest insects have been of the *colonization* type: a relatively small colony of a new parasite species is established in a region where it is expected to become a permanent part of the natural control complex.

Inoculative releases are periodic releases in which control is dependent upon progeny being produced for more than one generation following colonization. They are usually made to establish an enemy in areas from which it is temporarily absent due to adverse environmental conditions, and they have been used against agricultural and horticultural pests (*DeBach and Hagen 1964*), but not in forestry. Integrated control of pests of trees at the periphery of the range of effective parasite species might well involve such inoculative releases. In addition, inoculative releases early in the development of an outbreak could be used to speed parasite response to pest population increases.

Inundative releases are also periodic, but are made to control a pest by the actions of the natural enemies released, not by their progeny. Their potential has not received much attention in forest entomology, but they might be used to advantage in relatively small areas where chemical insecticides are undesirable but which are not suitable for the application of pathogenic insecticides: e.g., where the terrain, tree size, or stand density are unsuitable for the spray equipment. The application of this technique depends on the availability of large numbers of parasites at low cost. The egg parasite *Trichogramma* has

been used in this way against agricultural pests, and tests against the spruce budworm in western North America are now planned. Larval and cocoon parasites offer some promise for use in inundative releases in incipient outbreaks where damage caused by the target generation of the pest can be tolerated.

The enhancement of parasite effectiveness through environmental manipulation to eliminate or ameliorate conditions detrimental to the maximum expression of control potential of parasite species must play an important part in pest management. As a first step, the effects of poor timing or unnecessarily high kills associated with insecticidal control must be minimized. Integrated control will not progress far until the use of applications of chemical and biological insecticides at dosages causing nearly 100 percent mortality is confined to situations where such applications are essential: i.e., small areas of high-value crop with low damage thresholds and situations where eradication is possible. Insecticidal applications should be aimed at achieving the minimum mortality compatible with crop protection.

Information on the critical factors influencing the abundance of parasites and their ability to control their hosts is sadly lacking. The widely accepted idea that host abundance is usually the major factor controlling parasite abundance appears logically untenable in the light of studies of phytophagous species. Since many of the latter are prevented by other factors from fully exploiting their food source, we should expect a similar situation to exist for many parasite species. Studies of the population dynamics of parasitic species are badly needed to elucidate their controlling mechanisms.

The presence of special habitats, other than those occupied by their host, may be necessary for the survival of some parasite species. Flowering plants may be used as feeding sites for some species; e.g. two parasites of the European pine shoot moth leave the pines to dwell among the flowers of Umbelliferae (*Thorpe and Caudle 1938*), and the preoviposition period of female *Eucarcelia rutilla* is spent in oak rather than pine woods inhabited by its host (*Herrebout 1967*). The absence of

alternate hosts may limit the efficiency of some polyphagous parasites, particularly where a univoltine host is attacked by a bivoltine parasite. Increased parasite effectiveness might be attained by providing suitable alternate hosts, perhaps by encouraging plant species on which they feed. Other possibly limiting aspects of the environment which might be manipulated by management techniques are: shelter for overwintering parasite adults; protection from biotic enemies (e.g., ants), and improvement of the physical environment through the encouragement of specific plant growth for shelter.

Another opportunity for improving the efficiency of parasites lies in the selection of superior genetic strains for release against the target pest. This approach has been used in Manitoba against the larch sawfly. Muldrew (*1953*) showed that the larch sawfly in Manitoba was capable of encapsulating and killing the eggs of *Mesoleius tenthredinis*. This resistant strain has since spread until it now occurs from northeastern British Columbia to Nova Scotia. Experimental testing of *M. tenthredinis* from Europe and Japan revealed that the *M. tenthredinis* from Bavaria was capable of overcoming the encapsulation reaction of "resistant" larch sawflies and that this ability was inherited by the progeny of Canadian and Bavarian crosses. In 1963 and 1964, releases of Bavarian *M. tenthredinis* were made at two locations in Manitoba, and the encouraging results to date suggest the *M. tenthredinis* may again contribute to the control of the larch sawfly (*Turnock and Muldrew, in press*).

Selection of parasite strains also may be useful where bivoltine parasites attack univoltine hosts. If suitable alternate hosts are not available, relocation or development of a univoltine strain may be possible. We also can contemplate the use of secondary and tertiary parasites to improve the effectiveness of an existing parasite complex. Secondaries might be used to reduce the competitive stress of an ineffective primary on a potentially effective one. Tertiary parasites might reduce the deleterious effects of a secondary parasite on a primary.

The opportunity to use parasites to actively enhance the effectiveness of other control measures would appear to be limited, at present, to the introduction of a parasite species capable

of acting as a vector for an effective pathogen. Such a relationship now exists between the effective introduced parasites and the virus disease of the European spruce sawfly in eastern North America (*Neilson et al., in press*). The virus introduced against the European pine sawfly lacks an effective dispersing agent and is at present effective only as an insecticidal spray (*Griffiths et al., in press*). The selection and introduction of a parasite with the ability to disseminate this virus might improve the level of total control.

The integrated control approach to the management of a particular pest species may include active measures to increase the efficacy of enemies through release and enhancement programs or may merely avoid the use of other controls that decrease efficacy. In either case, no intelligent strategy can be developed without knowledge of the composition and effectiveness of the enemies in various guilds. The selection of parasites for release programs should be based on the comparison of guilds in the donor and recipient areas while enhancement programs would benefit from comparative studies of guilds in different stands and climates.

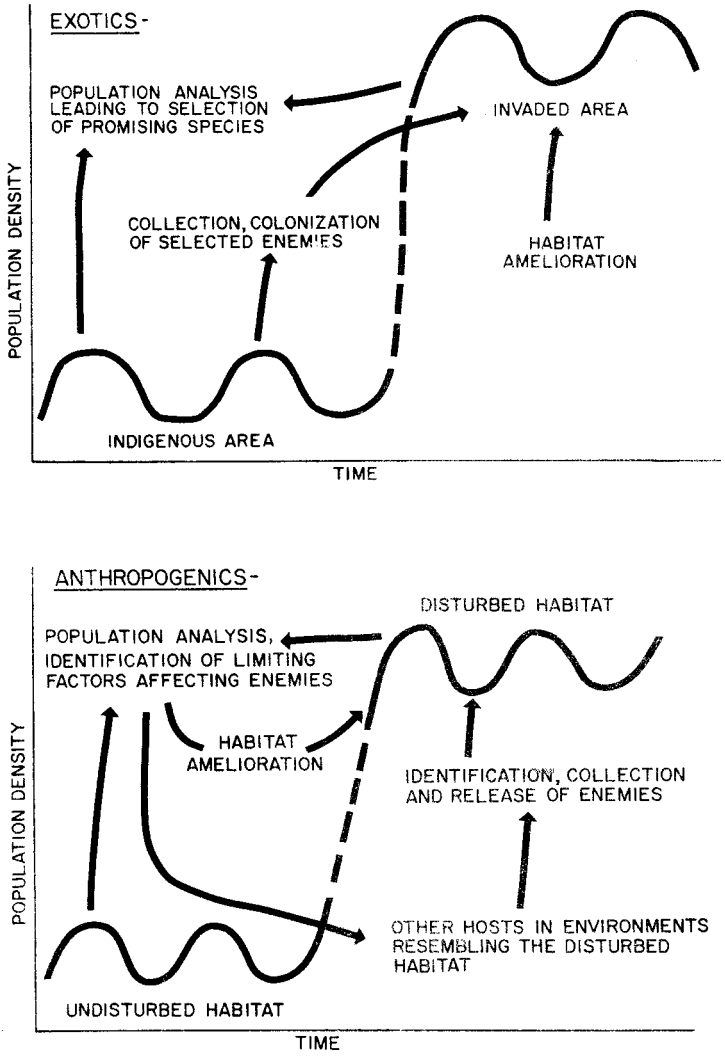
The place of parasites in integrated control operations would appear to vary with the type of pest. We would stress the importance of population analysis leading to the identification of ineffective guilds as a first step in planning the integrated control of any type of pest (fig. 1).

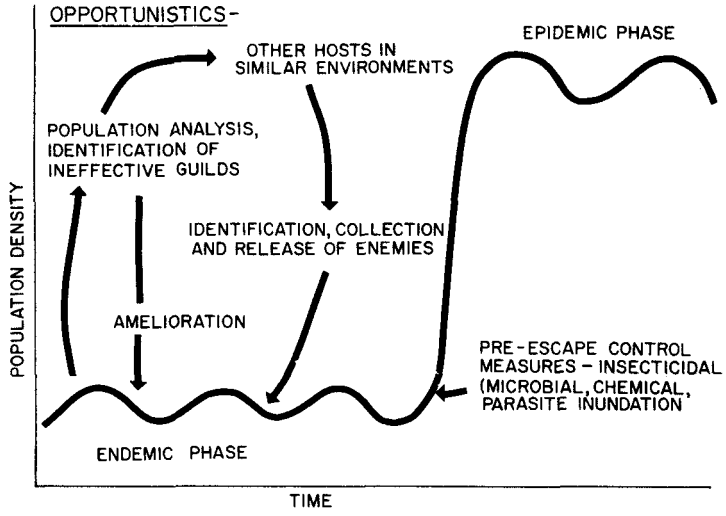
The identification and release of promising parasite species for colonization releases appears to be the most useful approach to the integrated control of exotic pests (fig. 1A). Insecticidal practices that would obstruct parasite establishment or effectiveness should be avoided. If habitat conditions in the invaded area appear suboptimal for otherwise preferred parasite species, habitat amelioration may also be considered.

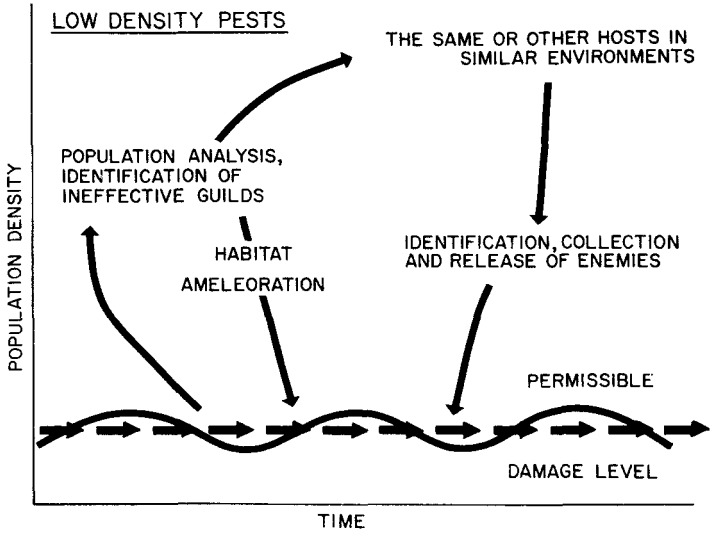
Although not all exotic pests are under effective economic control throughout their indigenous area, effective parasites may still be found for colonization releases. For example, the larch sawfly is anthropogenic in Europe while in North America it is a pest of undisturbed forests. Material for the recent release of the apparently effective parasite, *Olesicampe benefac-*

tor, was obtained in Europe from larch plantations where the larch sawfly was abundant as well as from native stands where it was consistently uncommon. Exotics that are opportunistic pests in their indigenous area may also offer an opportunity for

Figure 1.—Suggested strategy for biological and integrated control in relation to the population dynamics of four types of pests.







colonization of parasites. Here the basic assumption is that there are factors in the native home of the pest that inhibit parasite efficacy and that these inhibitors need not occur in the invaded area. Such factors may include hyperparasites, cleptoparasites (*Spradbery 1969*), predators, diseases, and competitors. In addition, differences between host trees and conditions of the physical environment in the new habitat as compared to

the native one may enhance the activity of certain parasite species.

With anthropogenic pests the main initial effort should be directed towards determining the reasons for the presence of control in natural habitats and the lack of it in modified habitats (fig. 1B). From this analysis the treatment required for rectification in the disturbed habitats may be evident. Such treatment may involve a cultural or stand-management approach or an attempt to enhance the effects of those biotic agents of control already present. It may involve a search in foreign areas for preadapted parasites of taxonomically or ecologically related hosts. Insecticidal applications will probably be necessary, but efforts should be made to ensure that the dosage and timing used are related to maximizing total control.

With opportunistic pests (fig. 1C), the initial effort should probably be on studies to determine whether the existing biotic factors, particularly those that act at endemic levels, can be enhanced. If this approach fails, a search in foreign lands for parasites of taxonomically or ecologically related species should be made. The possibility of forcing a change in the host preference of a parasite species that is not indigenous to the invaded area by cage parasitization and laboratory rearings should not be overlooked. The application of insecticides (chemical, microbial, inundative releases) during early phases of population build-up to prevent climatic release of the pest should be tested.

Since low-density pests are characterized by low-amplitude population fluctuations, (fig. 1D), improvement of the natural control complex may prove difficult. Colonization of new parasite species from other areas and enhancement of existing parasite efficacy may be possible, but the necessity for periodic control operations will probably remain. As an alternative to chemical and microbial insecticides, inundative releases of native parasites might be useful to avoid environmental contamination and application problems associated with biocides. In some cases, the most valid approach would be to promote public acceptance of a somewhat higher level of damage.

In conclusion, we would emphasize that although there has been considerable talk about the applicability of integrated con-

trol approaches to forest pest management, few attempts have been made. This approach has been successfully used against agricultural pests (see *Bartlett 1964; van den Bosch and Stern 1962*) particularly in orchards where conditions are similar to the forest ecosystem. Beirne (*1962*) suggested that neglect of the integrated approach was due to the amount and complexity of background information that must be gathered before the method becomes operational, the reluctance of growers to reduce applications of chemicals (or to suffer some damage while giving biotic agents a fair chance to build up), and the inability of proponents of opposite schools of thought to cooperate. We might also add that another contributing factor to this neglect may be that the method is still in its infancy and the knowledge and techniques necessary to enable its growth into vigorous adulthood still await discovery and development.

References

Andrewartha, H. G., and L. C. Birch
1954. THE DISTRIBUTION AND ABUNDANCE OF ANIMALS. 782 pp. Univ. Chicago Press, Chicago.

Auer, C.
1969. A SIMPLE MATHEMATICAL MODEL FOR "KEY-FACTOR" ANALYSIS AND COMPARISON. Swiss Federal Inst: Tech., Zurich. The working group on the population dynamics of *Zeiraphera diniana*. Commun. 34: 8 pp.

Balch, R. E.
1964. THE FUTURE IN FOREST ENTOMOLOGY. J. Forestry 62: 11-18.

Bartlett, B. R.
1964. INTEGRATION OF CHEMICAL AND BIOLOGICAL CONTROL. IN BIOLOGICAL CONTROL OF INSECT PESTS AND WEEDS. Ed. P. DeBach. pp. 489-511. Reinhold Publishing Corp., New York.

Beirne, B. P.
1962. TRENDS IN APPLIED BIOLOGICAL CONTROL OF INSECTS. Ann. Rev. Entomol. 7: 387-400.

Buckner, C. H.
1966. THE ROLE OF VERTEBRATE PREDATORS IN THE BIOLOGICAL CONTROL OF FOREST INSECTS. Ann. Rev. Entomol. 11: 449-470.

Buckner, C. H., and W. J. Turnock
1965. AVIAN PREDATION ON THE LARCH SAWFLY, PRISTIPHORA ERICHSONII (HTG.) (HYMENOPTERA: TENTHREDINIDAE). Ecol. 46: 223-236.

Clausen, C. P.
1956. BIOLOGICAL CONTROL OF INSECT PESTS IN THE CONTINENTAL UNITED STATES. USDA Tech. Bull. 1139, 151 pp.

Cole, L. C.
1966. THE COMPLEXITY OF PEST CONTROL IN THE ENVIRONMENT. IN SCIENTIFIC ASPECTS OF PEST CONTROL. Nat. Acad. Sci. Pub. 1402: 13-25. Washington, D.C.

DeBach, P.
1964. SUCCESSES, TRENDS, AND FUTURE POSSIBILITIES. IN BIOLOGICAL CONTROL OF INSECT PESTS AND WEEDS. Ed. P. DeBach. pp. 673-713. Reinhold Publishing Corp., New York.

DeBach, P. and K. S. Hagen
1964. MANIPULATION OF ENTOMOPHAGOUS SPECIES. IN BIOLOGICAL CONTROL OF INSECT PESTS AND WEEDS. Ed. P. DeBach. pp. 429-458. Reinhold Publishing Corp., New York.

Doutt, R. L. and P. DeBach
1964. SOME BIOLOGICAL CONTROL CONCEPTS AND QUESTIONS. IN BIOLOGICAL CONTROL OF INSECT PESTS AND WEEDS. Ed. P. DeBach. pp. 118-

142. Reinhold Publishing Corp., New York.

Dowden, P. B.
1962. PARASITES AND PREDATORS OF FOREST INSECTS LIBERATED IN THE UNITED STATES THROUGH 1960. USDA Agr. Handbook 226, 70 pp.

Embree, D. G.
1965. THE POPULATION DYNAMICS OF THE WINTER MOTH IN NOVA SCOTIA: 1954-1962. Entomol. Soc. Can. Mem. 46, 57 pp.

Griffiths, K. J., A. H. Rose and F. T. Bird
[In Press.] NEODIPRION SERTIFER (GEOFF.), EUROPEAN PINE SAWFLY (HYMENOPTERA: DIPRIONIDAE). IN BIOLOGICAL CONTROL PROGRAMS AGAINST INSECTS AND WEEDS IN CANADA, 1959-1968.

Herrebout, W. M.
1967. HABITAT SELECTION IN EUCARCELIA RUTILLA VILL. (DIPTERA: TACHINIDAE). I OBSERVATIONS ON THE OCCURRENCE DURING THE SEASON. Zeit. f. ang. Entomol. 60: 219-229.

Huffaker, C. B. and C. E. Kennett
1969. SOME ASPECTS OF ASSESSING EFFICIENCY OF NATURAL ENEMIES. Can. Entomol. 101: 425-447.

Huffaker, C. B. and P. S. Messenger
1964. THE CONCEPT AND SIGNIFICANCE OF NATURAL CONTROL. IN BIOLOGICAL CONTROL OF INSECT PESTS AND WEEDS. Ed. P. DeBach. pp. 74-117. Reinhold Publishing Corp., New York.

Ives, W. G. H., W. J. Turnock, C. H. Buckner, R. J. Heron and J. A. Muldrew
1968. LARCH SAWFLY POPULATION DYNAMICS: TECHNIQUES. Manitoba Entomol. 2: 5-36.

Klomp, H.
1966. THE DYNAMICS OF A FIELD POPULATION OF THE PINE LOOPER, BUPALUS PINIARIUS L. (LEP., GEOM.) Adv. Ecol. Res. 3: 207-305.

Liu, Chung-lo
1958. MONOPHAGY VERSUS POLYPHAGY IN THE CHOICE OF ENTOMOPHAGOUS INSECTS IN BIOLOGICAL CONTROL. Int. Conf. Insect Pathol. Biol. Control, 1st. Trans. 1958: 521-531. Prague.

Mattson, W. J., F. B. Knight, D. C. Allen, and J. L. Foltz
1968. VERTEBRATE PREDATION ON THE JACK PINE BUDWORM IN MICHIGAN. J. Econ. Entomol. 61: 229-234.

McGugan, B. M. and H. C. Coppel
1962. A REVIEW OF THE BIOLOGICAL CONTROL ATTEMPTS AGAINST INSECTS AND WEEDS IN CANADA. PART II. BIOLOGICAL CONTROL OF FOREST INSECTS, 1910-1958. Tech. Commun. 2, 35-216, C.I.B.C., Trinidad.

Miller, C. A.
1963. PARASITES AND THE SPRUCE BUDWORM. IN THE DYNAMICS OF EPIDEMIC SPRUCE BUDWORM POPULATIONS. Ed. R. F. Morris. Entomol. Soc. Can. Mem. 31: 228-244.

Miller, C. A.
1966. THE BLACK-HEADED BUDWORM IN EASTERN CANADA. Can. Entomol. 98: 592-613.

Miller, C. A. and T. A. Angus
[In Press.] CHORISTONEURA FUMIFERANA (CLEMENS), SPRUCE BUDWORM (LEPIDOPTERA: TORTRICIDAE). IN BIOLOGICAL CONTROL PROGRAMS AGAINST INSECTS AND WEEDS IN CANADA, 1959-1968.

Molnar, A. C., J. W. E. Harris and D. A. Ross
1966. BRITISH COLUMBIA REGION. IN REPORT OF THE FOREST INSECT AND DISEASE SURVEY. Can. Dep. Forestry and Rural Develop., Forestry Br. 108-123.

Morris, R. F.
1959. SINGLE-FACTOR ANALYSIS IN POPULATION DYNAMICS. Ecol. 40: 580-588.

Morris, R. F., ed.
1963. THE DYNAMICS OF EPIDEMIC SPRUCE BUDWORM POPULATIONS. Entomol. Soc. Can. Mem. 31, 332 pp.

Morris, R. F.
1969. APPROACHES TO THE STUDY OF POPULATION DYNAMICS. IN FOREST INSECT POPULATION DYNAMICS. USDA Forest Serv. Res. Paper NE-125: 9-28, illus. NE. Forest Exp. Sta. Upper Darby, Pa.

Muldrew, J. A.
1953. THE NATURAL IMMUNITY OF THE LARCH SAWFLY, (PRISTIPHORA ERICHSONII (HTG.)) TO THE INTRODUCED PARASITE MESOLEIUS TENTHREDINIS MORLEY, IN MANITOBA AND SASKATCHEWAN. Can. J. Zool. 31: 313-332.

National Academy of Sciences.
1969. PRINCIPLES OF PLANT AND ANIMAL PEST CONTROL VOL. 3 INSECT-

PEST MANAGEMENT AND CONTROL. Nat. Acad. Sci. Pub. 1695. 508 pp. Washington, D.C.

Neilson, M. M., R. Martineau and A. H. Rose
[In Press.] DIPRION HERCYNIAE (HTG.) EUROPEAN SPRUCE SAWFLY (HYMENOPTERA: DIPRIONIDAE). IN BIOLOGICAL CONTROL PROGRAMS AGAINST INSECTS AND WEEDS IN CANADA, 1959-1968.

Nicholson, A. J.
1954. AN OUTLINE OF THE DYNAMICS OF ANIMAL POPULATION. Aust. J. Zool. 2: 9-65.

Nicholson, A. J. and V. A. Bailey
1935. THE BALANCE OF ANIMAL POPULATIONS. Zool. Soc. London Proc. Part I: 551-598.

Prebble, M. L.
1960. BIOLOGICAL CONTROL IN FOREST ENTOMOLOGY. Entomol. Soc. Amer. Bull. 6: 6-8.

Pschorn-Walcher, H.
1963. HISTORISCH-BIOGEOGRAPHISCHE RUCKSCHLUSSE AUS WIRT-PARASITEN-ASSOCIATIONEN REI INSEKTEN. Zeit. f. ang. Entomol. 51: 208-214.

Pschorn-Walcher, H.
1964. COMPARISON OF SOME DREYFUSIA (=ADELGES) INFESTATIONS IN EURASIA AND NORTH AMERICA. Commonwealth Inst. Biol. Contr. Tech. Bull. 4: 1-23.

Pschorn-Walcher, H. D. Schroder and O. Eichhorn
1969. RECENT ATTEMPTS AT BIOLOGICAL CONTROL OF SOME CANADIAN FOREST INSECT PESTS. Commonwealth Inst. Biol. Contr. Tech. Bull. 11: 1-18.

Root, R. B.
1967. THE NICHE EXPLOITATION PATTERN OF THE BLUE-GRAY GNATCATCHER. Ecol. Monogr. 37:317-350.

Simmonds, F. J.
1956. THE PRESENT STATUS OF BIOLOGICAL CONTROL. Can. Entomol. 88: 553-563.

Spradbery, J. P.
1969. THE BIOLOGY OF PSEUDORHYSA STERNATA MERRILL (HYM., ICHNEUMONIDAE), A CLEPTOPARASITE OF SIRICID WOODWASPS. Ent. Res. Bull. 59: 291-297.

Stark, R. W.
1959. POPULATION DYNAMICS OF THE LODGEPOLE NEEDLE MINER, RECURVARIA STARKI FREEMAN, IN CANADIAN ROCKY MOUNTAIN PARKS. Can. J. Zool. 37: 917-943.

Syme, P. D.
[In Press.] RHYACIONIA BUOLIANA (SCHIFF.), EUROPEAN PINE SHOOT MOTH (LEPIDOPTERA: OLETHREUTIDAE). In Biol. Contr. against Insects and Weeds in Canada, 1959-1968.

Taylor, T. H. L.
1955. BIOLOGICAL CONTROL OF INSECT PESTS. Ann. Appl. Biol. 42: 190-196.

Thorpe, W. H., and H. B. Caudle
1938. A STUDY OF THE OLFACTORY RESPONSES OF INSECT PARASITES TO THE FOOD PLANT OF THEIR HOST. Parasitology 30: 523-528.

Turnbull, A. L. and D. A. Chant
1961. THE PRACTICE AND THEORY OF BIOLOGICAL CONTROL OF INSECTS IN CANADA. Can. J. Zool. 39: 697-753.

Turnock, W. J.
1969. PREDATION BY LARVAL ELATERIDAE ON PUPAE OF THE PINE LOOPER, BUPALUS PINIARIUS (L). Netherlands J. Zool. 19: 393-416.

Turnock, W. J. and J. A. Muldrew
[In Press.] PRISTIPHORA ERICHSONII (HTG.), LARCH SAWFLY. (HYMENOPTERA: TENTHREDINIDAE). In Biol. Contr. Programs against Insects and Weeds in Canada, 1959-1968.

van den Bosch, R. and V. M. Stern
1962. THE INTEGRATION OF CHEMICAL AND BIOLOGICAL CONTROL OF ARTHROPOD PESTS. Ann. Rev. Entomol. 7: 367-386.

Varley, G. C. and G. R. Gradwell
1970. RECENT ADVANCES IN INSECT POPULATION DYNAMICS. Ann. Rev. Entomol. 15: 1-24.

Watt, K. E. F.
1968. ECOLOGY AND RESOURCE MANAGEMENT. 450 pp. McGraw-Hill Book Co., New York.

Wolcott, G. W.
1958. THE EVANESCENCE OF PERFECT BIOLOGICAL CONTROL. 10th Int. Congr. Entomol. 1956 Proc. 4: 511-513. Montreal.

Zwolfer, H.
1961. A COMPARATIVE ANALYSIS OF THE PARASITE COMPLEXES OF THE EUROPEAN FIR BUDWORM, CHORISTONEURA MURINANA (HUB.) AND THE NORTH AMERICAN SPRUCE BUDWORM, C. FUMIFERANA (CLEM.). Commonwealth Inst. Biol. Control. Tech. Bull. 1: 1-162.

INSECTICIDES

by CARROLL B. WILLIAMS, Jr., and PATRICK J. SHEA

INSECT PEST PROBLEMS have increased substantially during the past two decades in agricultural crop systems and, to a much lesser extent, in certain forest ecosystems. According to Stern *et al. (1959)*, several factors have contributed to this increase in insect pest problems: (1) the transportation and establishment of foreign pests without their natural enemies; (2) the rise of new pests due to the widespread cultivation of their favorable host plants; (3) the increasing use of crop monocultures because of their economical planting and harvesting advantages; and (4) the advent and widespread use of the inorganic insecticides, particularly DDT, to directly suppress insect pest populations.

Initially the inorganic insecticides were spectacularly successful in suppressing agricultural insect pests and insect vectors of various human diseases. However, the subsequent resurgence of pest populations to even higher general equilibrium levels, the rapid development of resistance to insecticides, and the growing contamination of the environment by the persistent chlorinated hydrocarbons showed these insecticides to be a mixed blessing (*van den Bosch 1970*). Ironically, some agricultural pests were previously effectively controlled by their parasites and predators. But the use of biotic agents gave way to DDT.

The spotted alfalfa aphid story in California in the mid-50's, the *Heliothis* and aphid story in cotton in the Canete Valley of Peru (*Kilgore and Doutt 1967*), and the apple orchards of Nova Scotia (*Pickett and MacPhee 1965*), are all examples of the consequence of relying solely on pesticides for protection of crops.

The common result of these pesticide programs was the virtual elimination of the natural enemies of the pests, followed by resurgence of the pest populations; the development of resistance to insecticides by the target pests; outbreaks of secondary pests; increasing costs of pesticides due to more frequent applications; greater amounts of pesticides per application, involving, of course, the recurrent costs of equipment, labor, and materials; residue hazards and legal complications—and still no satisfactory control. Eventually pest-management systems were evolved for a few of these pests. In each of these situations chemical, biological, cultural, and regulatory methods were used to keep the various pest populations below the economic injury levels for the crops (*Pickett and MacPhee 1965*).

Forest Insect Pests

Forest entomologists also have shown an increasing reliance on chemicals in pest control. Beginning in 1948, the spruce budworm species complex has been sprayed in various forests from New Brunswick to Oregon with varying degrees of success (*Eaton et al. 1949; Morris 1951 b; Benedict 1959*).

Epidemic populations of the gypsy moth, the Great Basin tent caterpillar, and the Douglas-fir tussock moth have also been aerially sprayed with various degrees of effectiveness (*O'Dell 1959; Benedict 1959*). Some bark beetle populations have been suppressed by applications of insecticides on the boles of infested trees (*Massey et al. 1953; Wygant 1959*).

Frequent applications of insecticides were required to bring a certain number of undamaged trees within plantations through the life growth stages when they are highly susceptible to economic injury from plantation insects such as the white-pine weevil (*Marty and Mott 1964*). European pine shoot moth, and various sawflies. Also, the increasing establishment of high-quality seed orchards required a heavy reliance on insecticides to control forest cone and seed insects (*Merkel 1969*).

Although there was a definite shift toward heavier reliance on chemicals—particularly DDT—during the last two decades to control forest insect pests, insecticides have never been as fre-

quently and consistently applied to forest ecosystems as they have been to agro-ecosystems. This is because: (1) there generally has not been the need; and (2) there is not the crop value.

There has not been the need because natural forest ecosystems, being much more complex and generally more stable than agro-ecosystems, are able to support numerous general as well as specific natural enemies (parasites and predators) of phytophagous forest insects, the category that practically all our forest insect pests arise from (*Franz 1966*). These biological control agents, collectively, have effectively dampened the population fluctuations of their hosts to the extent that most of the host insects seldom become economically important pests.

Young coniferous forest plantations resemble the simple agricultural systems. Although the insect fauna changes as plantation trees grow (*Martin 1965b, 1966; Gagné and Martin 1968*) plantation ecosystems remain relatively simple until thinning operations and other forms of tree mortality allow enough light to get to the forest floor. This permits other plant species to become established, which in turn attracts additional insect and other animal forms. Diversity in tree and other plant species and age groupings within a particular tree species helps create forest conditions such that extensive forested areas are not all equally susceptible at the same time to the same pests (*Craighead 1923*). In contrast, this high degree of susceptibility to one species of pests annually exists in agro-ecosystems.

Forest trees, being long-lived, are attacked at their various life stages by different insect pests (*Waters 1969*). Although most of these pests infrequently cause economic injury, there are several that do. It is seldom that several chemical treatments are required to get a forest stand (usually a plantation) through a growth stage vulnerable to a specific forest insect pest.

Cost Effectiveness

The valuation of annual agricultural crops greatly exceeds the annual return from forest crops such as timber and pulpwood. Consequently, the effectiveness of chemical treatments and costs of protecting these forest crops must be carefully consid-

ered. It is much more likely for protection costs to exceed the value protected in forestry enterprises than agricultural ones. Forest protection costs, as well as cultural treatments that do not immediately pay for themselves, are debits held against forest crops that may not be harvested for some time. These expenditures and the annual interest charges are carried until the value for these treatments (and there may be several) is realized at harvest time. Few businesses can afford this financial load and postponement of income. Fire, insects and diseases, and changing economies makes forestry a particularly risky business enterprise.

Insecticides should be used only in emergency situations and only when they are economically justifiable. One of the primary difficulties we have in forest insect control is determining economic thresholds for various forest pests. The economic threshold is that level of pest population that would cause economic injury without control (*Stern et al. 1959*). Economic injury is that level of damage at which the value exceeds the costs of control (*Stern et al. 1959*). Economic thresholds vary widely from area to area and depend on forest types, management intensity, and man's changing scale of economic values. Forest economic thresholds are infinitely compounded when we consider the values of the various forest resources aside from timber, such as watershed, wildlife, recreation, range, etc. Economic thresholds also depend on variations in consumer demands, and difficulties of measuring the impact of insects on yield and quality of the resource.

Environmental Contamination

Many of the insecticides applied on agricultural fields are aerially applied by planes flying close to the ground, thus minimizing spray drift out of the target area. However, environmental contamination from spraying agricultural fields is large and widespread. Insecticides affect the organisms in the target areas and are also transported through soil, air, and water to affect organisms miles from the target area. Insecticides have killed song and game birds in or near agricultural fields. Insecticides have seeped through soils and entered all water ways, re-

sulting at times in high fish kills (*U.S. Public Health Service 1961*).

The aerial application of insecticides to pest-infested forests affects not only the pest populations but also many other animals in the forest. These animals can be affected directly by actual contact with the insecticide spray droplet or residue and also indirectly through various food chains via environmental contamination. The applications of DDT against epidemic spruce budworm populations in Canadian forests have also affected the Atlantic salmon fisheries (*Kerswill 1958*) and the summer colonies of woodcock, which were subsequently exposed to heptachlor on their wintering grounds in the southern United States (*Wright 1960; DeWitt et al. 1960*). These are only two examples of non-target organisms being hurt from environmental contamination of forest insect control. The death of songbirds directly from DDT applied to elm bark beetle populations and indirectly through contamination of their food chain is yet another example (*Wallace et al. 1961; Barker 1958*).

The solution to these problems does not include the elimination of insecticides in forest insect control. If this were done at this time we would lose to those insects whose populations are not well regulated by natural factors but whose populations may frequently rise to the limit of their food supply and thereby completely deprive man of certain forest resources for a long time. Rather than propose the elimination of insecticides, we should use the ones that are currently available more intelligently and judiciously to avoid the kind of problems that have occurred in both agro-ecosystems and forest ecosystems. In this regard we also must closely examine our insecticide testing, registration, and labeling measures. We must also begin to develop more ecologically acceptable insecticides.

Ecologically Crude Insecticides

Most of the insecticides used widely today are environmentally crude. Broad-spectrum toxicological properties and marketing considerations were the major criteria applied to their development (*van den Bosch 1970*). The major objectives of the screening of these insecticides on various pests were to obtain

estimates of their killing efficiencies and residue data. Additional testing was done on an enlarged list of pests, on certain wildlife species, and on certain crop plants to determine any phytotoxicity effects. Until just recently, no data were obtained or required on the impact of these ecologically crude insecticides on the insect communities associated with the target pest populations. The importance of these data is emphasized when one recalls that insecticides used in suppressing forest insect pests were simply taken from agricultural use and applied to infested forests. Impact data are not pertinent to federal registration and the ultimate labeling of these chemicals. As a result, insecticide labels do not indicate that because of ecological impact the insecticide can, in some situations, lead to aggravated pest problems. Consequently, broader ecological criteria must be applied to the registration of broad-spectrum insecticides.

One registration requirement calls for recommended dosages of chemicals for use against various pests. There is no guarantee that the recommended dosage is the minimum effective dosage against that particular pest insect. Some of the recommended dosages for several of the organophosphates are at the upper limit of safety. If they are exceeded, serious kill of wildlife may result.

In this advanced technological country there is little reason why scientists could not predict the impact of different classes of insecticides on various ecosystems. There must be much greater understanding by chemists, entomologists, and wildlife ecologists of the interrelationships of a pesticide with soil, air, water, and living organisms to properly evaluate hazards to nontarget organisms and their environment. Each insecticide must be viewed in context with its properties, commercial usage, dosage, and the environmental effects. Predictions of the fate of each insecticide in various environments and its effects on target and nontarget organisms can be made on the basis of correlating toxicological, chemical, physical, and biochemical properties for each insecticide with the physical environment and representative phylla and orders of organisms treated. Each insecticide will differ in its uses, properties, advantages, and restrictions. We already have guidelines for evaluating the

properties of pesticides for safe use in the wildlife environment (*Kenaga 1968*).

What kind of insecticides can we design that would effectively suppress insect pest populations and still be ecologically acceptable? We have already discussed the ecologically crude insecticides that have contributed heavily to problems of resurgent, resistant pest populations and widespread environmental contamination. Obviously, there is a need for insecticides with different physical characteristics. Perhaps we can start by listing what we do not want, using DDT as an example:

1. DDT is chemically stable; half-life is more than 10 years.
2. Some of DDT's metabolites (DDE) are also exceedingly difficult to break down.
3. DDT has extremely low water solubility: less than 100 parts per million.
4. DDT is very soluble in lipids.
5. DDT is a broad-spectrum insecticide; many animal groups, not just insects, are harmed by it.
6. DDT readily forms suspensions in air and water.

The primary characteristic of DDT and its metabolite DDE responsible for most of our environmental problems is the combination of extreme persistence, low water solubility, and high lipid solubility. This combination of physical properties has allowed DDT to build up in many food chains and threaten the existence of animals at the higher trophic levels of these food chains. We can no longer apply extremely persistent insecticides to forest and agro-ecosystems. The use of persistent compounds must be restricted to product protection—fence posts, termite control, etc.

Desirable Characteristics

We think that generally we want more selective insecticides. There are insecticides that have relatively restricted toxicity range within Arthropoda. It is the broad toxicity to many groups of insects that is responsible for the elimination of the natural enemies (parasites and predators) of a phytophagous

pest along with the suppression of the pest populations. This has often allowed rapid resurgence of the phytophagous pest populations because they have been freed from the regulating effects of their natural enemies (*Kilgore and Doutt 1967*). The selective insecticides should have little effect on pollinators, decomposers, and aquatic organisms.

Selective insecticides will, for technological and economical reasons, become more costly to develop than existing broad-spectrum insecticides. But because they are ecologically selective, they will be used less intensively, effect better control of target pests, cause substantially fewer secondary pest problems, and be less conducive to the development of resistance in the pest species (*van den Bosch 1970*). Consequently, selective insecticides should be less costly to the user over the long run, and infinitely less hazardous to the general environment.

The development costs for ecologically acceptable insecticides will unquestionably be greater than those for the existing broad-spectrum, environmentally crude insecticides. Furthermore, the market potential for a given selective material will be considerably smaller than that for a broad-spectrum material.

The chemical companies will not want to bear the full cost of developing selective pesticides, and may even refuse to synthesize them. Because of this, the Federal Government may have to underwrite the development costs for the ecologically acceptable pesticides. Probably the required monies would not go directly to the chemical companies, but would be used to support critical developmental research by Federal agencies for studies concerned with the analyses of the material health hazards and their impact on the environment (*van den Bosch 1970*).

We believe the toxicity of an insecticide must be high to the target pest so that only a very small quantity of the material will need to be applied to obtain reasonable suppression of the target pest populations. In this way we can keep costs of applying it down and reduce the environmental pollution by not spraying large quantities of it per acre.

The material should be persistent enough to be available to the target pest. Perhaps its lethality should not degrade sub-

stantially before 24 hours have passed. Most insecticides that are aerially applied to forest and agro-ecosystems kill the pest by contact—either through the aerially borne insecticide droplet impinging upon the insect cuticle or the insect walking over the insecticide residue adhering to the host plants. Persistence should be long enough to allow those insects missed by the droplets to crawl over the residue and succumb to a lethal dose. The field effectiveness of DDT was due to its persistence in the habitat of the target pest insect. Unfortunately, it was so persistent that when the plant decayed, DDT was still present in the environment but no longer available to the target pest insect. In contrast, pyrethrin compounds are often much more toxic to various insects than DDT, but most of these compounds are very instable and rapidly break down into harmless metabolites. Consequently, their field effectiveness is not high. In contrast, pyrethrin stabilized for approximately 4 to 8 hours has much greater field effectiveness.

Improved Application

Another way we can increase the effectiveness of insecticides and reduce their pollution of the environment is by improving our application of the materials to the pest-infested crops. Application techniques are just as important as the insecticide. The chemical is just one factor in a complex system that includes spray physics and equipment, the timing of application, and a thorough knowledge of the weather conditions during the spray operations, as well as a complete knowledge of the target pest and its most susceptible stage.

It is important that a contact insecticide be applied during a period when the majority of the insect pest population is exposed. For many defoliating insects, this is during the larval stage, particularly at the large or late larval stage. Frequently, about 75 percent of the food consumed by insect larvae is consumed during the last larval instar. Also, it is not wise to spray when parasites of the target pest are vulnerable. Consequently, compromises are sometimes required between applying the insecticide when the target insect is most exposed to obtain a

very high population kill, or applying earlier in the larval stages of the pest to save as much foliage as possible, realizing that you would obtain less population kill, but at the same time would protect the parasites of the target pest.

Application of the insecticide must be made to assure that the target area is adequately covered—that no areas are missed and that few overlaps occur. Well-marked spray boundaries and preplanned flight lines are very helpful. Observation planes are useful in guiding spray planes during their runs to note the drift of the insecticide clouds, thermal updrafts, and missed areas.

Atmospheric conditions must be right for the aerial application. Spraying is usually done early in the morning when the wind speed is less than 5 m.p.h. and there are no thermal updrafts caused by the sun warming the slopes. Spraying is discontinued when the wind speed or turbulence increases, because excessive drift of the spray cloud will cause areas to be missed and contamination of nontarget areas to occur.

Recent research indicates that practically all the insect mortality in an aerial application is caused by spray droplets that are below 50 microns in size when they contact the target insect (*Himel and Moore 1967*). In the past, spray droplets of this size usually represented a small portion of the spray droplet spectrum and contained approximately 5 percent of the spray mass. This means that 95 percent of the spray mass in droplets over 50 microns was wasted and contaminated the environment. The magnitude of this waste is illustrated by the fact that doubling droplet diameter results in an eightfold increase in volume. That is, a 100-micron drop contains 8 times as much insecticide as a 50-micron drop. It is simply a matter of spray physics—double the size of the droplets and you cube their volume. The insect larvae are screened by foliage, limbs, tree trunks, and silken threads, which filter out the larger spray droplets. Possibly those droplets 50 microns and smaller that reached the forest canopy were slightly repelled by the small magnetic fields surrounding the foliage and small limbs, filtered through the forest canopy, and scored direct hits on the insect larvae.

These spray droplets 50 microns and under in size have been referred to as aerosol sprays. Weather will be an important

factor in aerosol spraying. Air currents can be used to deliver the spray to the target area by a process called atmospheric transport and diffusion (A. D. Moore, 1967; personal communication). Atmospheric diffusion is accomplished when the aerosol spray is spread out laterally over a drainage like a flat cloud. This occurs when the air is still under inversion conditions.

Atmospheric transport is the movement of the spray cloud down toward the ground into the tree crowns. This is accomplished when the sun begins to warm the east-facing mountain slopes early in the morning. As the low-lying air warms up and begins to rise, it is replaced by air moving in. A mixing or looping effect occurs, which sends the spray droplets into the tree crowns several times at various angles. Therefore, we need to develop spray equipment that will discharge the spray mass in that portion of the droplet spectrum that is most effective in reaching and killing the target insect. The timing of the spraying application must be at the optimum stage when the target pest is vulnerable; and its parasites and predators must be protected before substantial economic injury occurs. The spray must be applied in a manner conducive to reduction of environmental contamination.

Strategy of Pest Management

Not only are insecticides and application techniques important factors in a pest-management system, but also pest control strategies should play an increasing role in pest management. Research in the population dynamics of various pests and in the growth and development of their host stands should provide data from which we can construct models describing pest and resource systems. Reliable models will describe the behavior of the pest system responding to its natural mortality factors. These models should describe the interaction between various pest population densities and the forest system. Simulation studies involving the interaction between these systems need to be run through many simulated insect generations to determine what happens to both systems at different population levels and various forest-stand damage histories.

These simulation studies should: (1) determine the effects of various pest population levels on current and cumulative damage in the absence of and with varying degrees of chemical control; (2) describe the effectiveness of various natural mortality factors at different pest populations in the absence of chemical controls; (3) determine which mortality factors are key factors under various simulated forest stand conditions; (4) affect various levels of insecticide-induced mortality on the pest populations to describe the effectiveness of natural mortality factors at these different pest population levels with the added presence of the insecticide and its impact on the environment; (5) determine the cost effectiveness of various classes of insecticides on the pest populations and the forest stands; (6) determine the impact of these various classes of insecticides on certain nontarget organisms and the environment; (7) determine the optimum timing of various classes of insecticides that will minimize the hazards to the parasites and predators of the pest and maximize crop protection; and (8) determine the minimum pest population levels needed to maintain effective parasite and predator activity.

Various pest-control strategies can be developed from information obtained from these simulation studies. We must know what happens to forest stands infested by various pest population levels for different periods of time. We must be able to predict the effectiveness of various classes of pesticides and their hazards to the environment, based on their properties, the pest population levels, and the type and conditions of the infested forest stands.

We must apply the insecticide in such a manner that it has little effect on the other mortality factors affecting the target-pest populations. This means that the insecticide by itself may not be applied at a time that could result in maximum pest mortality. Certain constraints like the vulnerability of effective parasites and predators at various stages of the target pest's life cycle would require insecticides being applied at a time when these natural enemies are less vulnerable even though the timing of the spray application is such that the pest is also less vulnerable to the insecticide. The goal in pest management is

not pest eradication but the maintenance of pest population levels below the economic injury levels of our various resources.

Possibilities of Integrated Control

Since forest pest-control specialists are returning to an ecological approach to pest control, consider the general possibilities for using integrated control on several groups of insects.

The large investment necessary for the establishment of orchards comprising superior genotypes of various tree species for the purpose of high-quality seed production must be protected. The economic threshold for these orchards is quite low. Until more is known about the biology and population dynamics of cone and seed insects there will continue to be a heavy reliance on relatively persistent insecticides to suppress cone and seed insect populations in these orchards.

Since there is little or no investment for seed production in natural forests, there is little need for control of seed and cone insects. The economic threshold for seed production is very high.

The large investment for nursery establishment and production must also be protected. Integrated control of nursery pests is obtained by judicious nursery practices emphasizing hygiene, planting schedules, and various spot pesticide treatments (*Franz 1966*). Environmental contamination from the use of pesticides should be low.

The investment in plantation establishment can be won or lost depending upon the tree species planted and the site quality of the land. For example, the white-pine weevil precludes the planting of pure stands of eastern white pine throughout its botanical range. Shoot and tip moths endanger many plantations of hard pines in the eastern and southern United States. In contrast, many plantations of Douglas-fir in the Pacific Northwest thrived. So far, there has been little or no research on the population dynamics and parasites and predators of our plantation insects. Except for some virus diseases in some sawfly populations, biological control seems ineffective (or undeveloped) for most plantation insects. Varying the spacing of

seedlings—and subsequently stand density—may help decrease the damage from white-pine weevil and European pine shoot moth.

The mistake of planting large areas to pure stands of white pine and red pine should be avoided in the future. However, for the time being, many plantation owners rely on insecticides to bring through enough undamaged trees to make a profitable crop through the growth stage of susceptibility to plantation insects. Examination of old plantations formerly infested with shoot or tip moths frequently reveals that many trees, now pole-size, have outgrown deformities caused by these insects. Slow-growing trees on poor sites take longer to grow out of stages most susceptible to plantation insects. All in all, there appears to be an undeveloped opportunity for effective integrated control.

The combined use of silvicultural cutting techniques and pheromones, insecticides, and chemical sterilants promises an effective integrated control program for bark beetles within the *Dendroctonous* and *Ips* species complex.

Silvicultural techniques such as diversifying tree species within a forest stand and age groups within a tree species, can result in a mosiaic forest stand in which only a few portions are highly vulnerable at the same time to bark beetles. Risk-rating schemes such as the Keen classification and prompt salvage of blowdowns and rapid harvest of overmature stands helps to prevent bark beetle population build-ups in the most vulnerable trees.

The phermomone work offers the great possibility of attracting the beetles to a trap in which they may be killed by insecicides or sterilized by other chemicals. Some research breakthroughs are imminent.

Research is progressing on the population dynamics of various bark beetle species. The effectiveness of various parasites and predators is being assessed. There may be opportunities for manipulating these biotic agents to increase their effectiveness.

Generally speaking, the possibilitities of using integrated control on forest defoliating insect populations is good. Many of

the insects are effectively controlled by parasites and predators and only occasionally become numerous enough to require the application of insecticides. Current research on the population dynamics and sex pheromones of the most economically important insects promises substantial payoffs.

Some possibilities of an integrated control program for the most economically important forest defoliating insects are presented below.

Spruce Budworm Species Complex

Implicit in any ecological approach to pest control is knowledge of the biology and population dynamics of the insect itself. The spruce budworm species complex is widely distributed in North America. It spans the North American continent with representatives in many different forest types. It has been divided by T. N. Freeman (*1967*) into nine species.

The spruce budworm *Choristoneura fumiferanae* (Clemens) is the most widely studied forest defoliating insect pest in North America. A large portion of some of the most classical work in forest entomology has been done on this insect (*Morris 1963*).

A substantial amount of information exists on epidemic dynamics of *C. fumiferanae* in a few forest types. The majority of Canadian and American studies have been on epidemic populations of this insect in eastern North America balsam fir-white spruce forests. More work is needed on other *Choristoneura* species in other forest types. Although research on the 2-year budworm *C. biennis* populations in Canada has been published (*Shepherd 1959*), additional studies on *C. occidentalis* populations in Idaho, Montana, and the Pacific Northwest are necessary.

Very little published information on endemic population dynamics exists for any forest types. Biotic factors may be more effective in regulating low or endemic populations than high populations.

Several environmental factors seem to permit outbreaks of the eastern spruce budworm (*Choristoneura fumiferanae*) and the western budworm (*C. occidentalis*).

Dense populations of *C. fumiferanae* are associated with flowering of balsam fir, large areas of essentially pure balsam fir, mature and overmature balsam fir in mixed stands. White, red, and black spruce are also hosts. Spruce budworm larvae development may be more rapid on white spruce than on balsam fir.

C. occidentalis primary hosts are true firs, Douglas-fir, and Engelmann's spruce. Budworm-susceptible forests are increasing in Western States due to the logging of ponderosa pine and forest succession from pine to firs in the absence of fires. Population dynamics of *C. occidentalis* on true firs may be analogous to that of *C. fumiferanae* populations on balsam fir.

Hot dry weather is the key factor in large budworm outbreaks. Hot dry weather increases flowering in balsam fir trees over large areas, thereby resulting in optimum food and shelter for small budworm larvae. Budworm development, feeding activity, and survival are greater during hot dry weather. Any forest type and stand structure that allows high evaporation rates and increases crown exposure favors local survival of large budworm larvae regardless of regional weather.

It is desirable to identify, evaluate, and manage epicenters or reservoirs of pest populations, particularly when they are small in relation to the total potential infested area. Identification of epicenters has been done from time to time:

1. Lake Nipigon, Ontario—the area from which the huge outbreak during the early part of this century originated and gained momentum. Mature stand of balsam fir is now present.

2. Colorado Pass-Clearwater area Idaho—Montana. Budworm populations on grand fir sprayed five times to no avail as populations regained epidemic status within 2 years after spraying.

3. True fir concentrations in the Wallowa Mountain Ranges of eastern Oregon were the epicenters from which the 1945-55 budworm outbreak spread in Wallowa County.

Silvicultural Control

One of the procedures we may employ in manipulating the environment to make it less conducive to budworm population build-up is forest cutting. We usually call this procedure silvicultural control. The following is what might be attempted using this procedure. Many of the suggestions for eastern North America are well documented in the literature (*Morris 1963*).

In eastern North America:

1. Reduction of balsam fir complement in forest stand. Encourage less budworm-susceptible conifers and some hardwoods to achieve diversified forest types, thereby breaking up continuous canopies of balsam fir.

2. Cutting large overmature trees, and planning short rotations for pure balsam fir stands and mixed fir stands. The cutting units should be kept small (40 to 60 acres) and arranged to attain a diversification in age classes between adjacent units in succeeding balsam fir forest stands. Controlled burning and scarification of the forest floor should be practiced to destroy the advanced balsam fir regeneration and expose the mineral soil to increase the complement of white spruce in the succeeding forest stand.

In western North America:

1. Reduction of the true-fir complement in all budworm-populated forest stands.

2. Cutting Douglas-fir and burning cutting units to favor ponderosa pine over all firs.

Patch clearcutting with cutting units kept as small as practicable should be used to increase first- and second-instar budworm dispersal losses. The highest mortality of the generation occurs during these dispersal periods. During dispersal periods larvae are more likely to land on host trees in a dense stand than in an open stand.

Biological Control Procedures

Parasites, predators, and diseases do not appear capable of suppressing epidemic spruce budworm populations (*Morris 1963*). However, some of these agents may be more effective at low or endemic budworm population dynamics and consequently our need for additional work is again illustrated. In any case, full control by parasites and predators is a biological rarity.

It may be possible to increase the complement of the seemingly ineffective natural enemies of the budworm. Perhaps some of the potentially more effective parasites are regulated by alternate hosts. Regardless of present levels of knowledge on parasites and predators, insecticide application, if possible, should be timed to avoid periods when the parasites are emerging and flying. Chemical procedures must be used in a manner that is least disruptive to biological control of actual and potential pests.

Chemical Procedures

Insecticides have been the main control used in our attempts to suppress spruce budworm populations.

The spruce budworm is the most destructive forest defoliating pest in North America. As a result more acres of budworm-infested forests have been sprayed than for any other defoliating pest in North America. Since 1949, tree mortality resulting from spruce budworm outbreaks has been reduced through extensive aerial spraying programs, using various formulations of DDT on budworm-infested forests in the United States and Canada.

Although generally good direct control of *C. occidentalis* population has been obtained by aerial application of DDT at an average cost of $1.00 per acre, widespread concern has grown over the adverse effects of residual DDT against nontarget organisms. This concern prompted some Federal agencies to discourage and frequently ban the application of DDT on Federal forest lands. Also there is evidence that spruce budworm populations in New Brunswick were developing more resistance to DDT formulations (*Randall 1965*).

Programs were set up to seek safer, more specific, and less

persistent insecticides to replace the wide-spectrum, environmentally persistent DDT (*Moore 1964*). Some of the insecticides tested in that program—DDD, Korlan, Sevin, and Malathion—were not as effective as DDT against the spruce budworm at similar dosage levels. Phosphamidon is effective against the budworm and is only 1/40th as toxic as DDT to young Atlantic and Pacific salmon. But it is extremely toxic to birds. Laboratory and field tests show that one of the most promising insecticides for budworm control is a carbamate called Zectran. Zectran appears to have many of the characteristics sought in the basic chemical. It is 100 times more toxic to spruce budworm in the sixth instar than DDT and hence can be applied in small amounts not hazardous to other forms of life. Zectran is especially safe to fish, birds, and small mammals. It is also nonpersistent, breaking down in sunlight within a few hours.

Since Zectran does not possess the persistence of DDT, a characteristic that contributed significantly to the field effectiveness of DDT, the application procedures must be re-evaluated and updated to take advantage of the physical characteristics of Zectran. Target selectivity and percent mortality can be increased by the manner in which the insecticide is applied.

Quite clearly, differences in persistence mean differences in the probability of contact with the target pest when comparable methods of application are used. The probability of contact can be increased by employing any combination of the following procedures:

1. Increasing the number of applications in a season.
2. Increasing the amount of toxic material per acre in an application.
3. Increasing the amount of carrier in an application.
4. Modifying the droplet spectrum to yield higher proportions of the insecticide in the effective droplet size range.

First, most of the insecticide applied in past programs was wasted in large drops that did not hit the budworm but contaminated the environment. Recent research shows that droplets below 50 microns are most effective in causing budworm mor-

tality. About 97 percent of the droplets found on dead larvae in field tests were below 50 microns (*Himel and Moore 1967*). Spray equipment is now being developed to produce droplets below the 50-micron size at the target insect. (Missouri Equipment Development Center, USDA Forest Service, Missoula, Montana.)

Second, these small droplets are carried to the budworm larvae by atmospheric transport and diffusion much more than the larger droplets, which are more apt to be filtered out by the forest canopies. Strict attention must be paid to normal diurnal wind patterns in the drainages to be sprayed in order for the cloud of insecticide to be more accurately directed to the target insects.

Large-scale field tests on which Zectran was applied at an average concentration of 0.15 lb. in 0.73 gal. of cycle oil: Methylene chloride (9:1) per acre showed that the material is capable of reducing budworm populations by 90 percent or better. These field tests also showed that Zectran is relatively specific in its action by reducing budworm populations to a much greater extent than most populations of insects associated with it in tree crowns (*Williams and Walton 1968*). We have differential mortality that favors nonpest insects.

The ratio between parasites and host was radically altered by Zectran. Budworm larvae parasitized by the overwintering parasites *Apanteles* sp. and *Glypta hariolus* survived the applications of Zectran proportionately better than unparasitized budworm larvae and larvae parasitized by other parasites (*Williams et al. 1969*). Consequently, the incidence of parasitization expressed as the number of parasites per 100 budworm larvae increased after the insecticide application.

It may be possible through integrating these various control procedures to keep budworm populations below the economic level by:

1. Reducing or converting budworm-susceptible forest types through logging and control of species composition by logging and burning.

2. Attaining a diversification of species and age classes to re-

duce the component of susceptible species and age groups in the stands. The frequency of budworm outbreaks in an area may thereby be reduced.

3. Judicious use of a nonpersistent and relatively specific insecticide on budworm outbreaks that do occur, to increase the incidence of parasitism in the budworm population, yet not to decrease the population's alternate hosts of the parasites in the environment proportionately more than the budworm. This type of development should increase the parasite pressure on the next budworm generation and hopefully this situation would endure for several budworm generations. Identification of those areas where the pest-parasite ratio is unfavorable and proper timing of chemical application is important.

It is no longer necessary or even desirable to achieve a high percentage of mortality (usually 95 percent or greater) of the pest population as has been the goal of past pest-control programs. Although there has been no analysis of the results of aerial spraying experience against spruce budworm, it is clear that a rather large, well-organized segment of forest industry in eastern Canada has found, through extensive spraying experience, that sacrificing high percentage mortality for good foliage protection is an acceptable strategy for control operations. We recognize that this objective may not be optimal but conclude that it is acceptable at least in some economic circumstances, and consider levels of population reduction near to and higher than the levels that have been accepted in eastern Canada.

In some control situations we may be satisfied with a mortality of 90 percent or lower so that we do not disrupt but perhaps enhance biological control action where the pest-parasite ratio is unfavorable. A high mortality percentage is not important *per se*, but a residual and subsequent population regulated below the economic damage level should be the goal.

References

Barker, R. J.
1958. NOTES ON SOME ECOLOLOGICAL EFFECTS OF DDT SPRAYED ON ELMS. J. Wildlife Manage. 22(3): 269-274.

Benedict, W. V.
1959. EVERY FORESTER HAS A STAKE IN FOREST INSECT SPRAYING. J. Forestry 57: 245-249.

Craighead, F. C.
1923. A BRIEF SUMMARY OF THE BUDWORM INVESTIGATIONS IN CANADA. J. Forestry 67: 300-304.

DeWitt, J. B., C. M. Menzie,
V. A. Adomaitis, and W. L. Reichel
1960. PESTICIDAL RESIDUES IN ANIMAL TISSUES. N. Amer. Wildlife Conf. Trans. 25: 277-285.

Eaton, C. B., J. A. Beal,
R. L. Furniss and C. F. Speers
1949. AIRPLANE AND HELICOPTER SPRAYING WITH DDT FOR SPRUCE BUDWORM CONTROL. J. Forestry 47: 823-827.

Franz, J. M.
1966. INTEGRATED CONTROL OF FOREST PESTS. F.A.D. SYMP. INTEGRATED PEST CONTROL. Proc. (1965): 65-76.

Freeman, T. N.
1967. ON CONIFEROPHAGOUS SPECIES OF CHORISTONEURA (LEPIDOPTERA: TORTRICIDEA) IN NORTH AMERICA. I. SOME NEW FORMS OF CHORISTONEURA ALLIED TO C. FUMIFERANAE. Can. Entomol. 99: 449-455.

Gagne, W. C. and J. L. Martin
1968. THE INSECT ECOLOGY OF RED PINE PLANTATIONS IN CENTRAL ONTARIO. I. THE COCCINELLIDAE (COLEOPTERA). Can. Entomol. 100: 835-846.

Himel, C. M. and A. D. Moore
1967. SPRUCE BUDWORM MORTALITY AS A FUNCTION OF AERIAL SPRAYING DROPLET SIZE. Sci. 156: 3779 (1250-1251).

Kenaga, E. E.
1968. GUIDELINES FOR EVALUATING THE PROPERTIES OF PESTICIDES FOR SAFE USE IN THE WILDLIFE ENVIRONMENT. DOWN TO EARTH. 23(4): 11-18, illus.

Kerswill, C. J.
1958. EFFECTS OF DDT SPRAYING IN NEW BRUNSWICK ON FUTURE RUNS OF ADULT SALMON. Atlantic Advocate 48(8): 65-68.

Kilgore, W. V. and R. L. Doutt.
1967. PEST CONTROL, BIOLOGICAL, PHYSICAL AND SELECTED CHEMICAL METHODS. 477 pp. Acad. Press, New York and London.

Martin, J. L.
1965b. THE INSECT ECOLOGY OF RED PINE PLANTATIONS IN CENTRAL ONTARIO. III. SOIL-SURFACE FAUNA AS INDICATORS OF STAND CHANGE. Ent. Soc. Intario. Proc. 95: 87-102.

Martin, J. L.
1966. THE INSECT ECOLOGY OF RED PINE PLANTATIONS IN CENTRAL ONTARIO. IV. THE CROWN FAUNA. Can. Entomol. 98: 10-27.

Marty, R., and D. G. Mott
1964. EVALUATING AND SCHEDULING WHITE-PINE WEEVIL CONTROL IN THE NORTHEAST. USDA Forest Serv. Res. Paper NE-19. 56 pp., illus. NE. Forest Exp. Sta., Upper Darby, Pa.

Massey, C. L., R. D. Chisholm and
N. D. Wygant
1953. ETHYLENE DIBROMIDE FOR CONTROL OF THE BLACK HILLS BEETLE. J. Econ. Entomol. 46: 601-604.

Merkel, E. P.
1969. INSECT CONTROL IN FOREST TREE SEED ORCHARDS. J. Forestry 67: 748-750.

Moore, A. D.
1964. PROGRESS OF INSECTICIDE SCREENING IN FORESTRY. PART II. INSECTICIDE EVALUATION PROJECT. WESTERN FORESTRY CONSERV. ASSOC. FOREST PEST COMM. Annu. Meeting 1964: 7-8.

Morris, R. F.
1951b. THE IMPORTANCE OF INSECT CONTROL IN A FOREST MANAGEMENT PROGRAM. Can. Entomol. 83(7): 176-181.

Morris, R. F. (Ed.)
1963. THE DYNAMICS OF EPIDEMIC SPRUCE BUDWORM POPULATIONS. Entomol. Soc. Can. Mem. 31, 332 pp., illus.

O'Dell, W. V.
1959. THE GYPSY MOTH CONTROL PROGRAM. J. Forestry 57: 271-273.

Pickett, A. D. and A. W. MacPhee
1965. TWENTY YEARS EXPERIENCE WITH INTEGRATED CONTROL PROGRAMS IN NOVA SCOTIA APPLE ORCHARDS. 12th Int. Congr. Entomol. Proc. 597. London.

Randall, A. P.
1965. EVIDENCE OF DDT RESISTANCE IN POPULATIONS OF SPRUCE BUDWORM, CHORISTONEURA FUMIFERANAE (CLEMENS), FROM DDT-SPRAYED AREAS OF NEW BRUNSWICK. Can. Entomol. 97: 1281-1291.

Shepherd, R. F.
1959. PHYTOSOCIOLOGICAL AND ENVIRONMENTAL CHARACTERISTICS OF OUTBREAK AND NON-OUTBREAK AREAS OF THE TWO-YEAR CYCLE SPRUCE BUDWORM. CHORISTONEURA FUMIFERANAE. Ecol. 40(4): 608-620, illus.

Smith A. F. and W. W. Allen
1954. INSECT CONTROL AND THE BALANCE OF NATURE. Sci. Amer. 190: 38-42.

Stern, J. M., *et al.*
1959. THE INTEGRATION OF CHEMICAL AND BIOLOGICAL CONTROL OF THE SPOTTED ALFALFA APHID. Part I. THE INTEGRATED CONTROL CONCEPT. Hilgardia 29: 81-101.

U.S. Public Health Service
1961. POLLUTION-CAUSED FISH KILLS IN 1960. U.S. DEPARTMENT OF HEALTH, EDUCATION AND WELFARE. Public Heath Serv. Pub. 847, 20 pp.

Van den Bosch, R.
1970. PESTICIDES: PRESCRIBING FOR THE ECOSYSTEM. Environment 12(3): 20-25, illus.

Wallace, G. J., W. P. Nickell and R. F. Bernard
1961. BIRD MORTALITY IN THE DUTCH ELM DISEASE PROGRAM IN MICHIGAN. Cranbrook Inst. Sci. Bull. 41; 44 pp.

Waters, William E.
1969. THE LIFE TABLE APPROACH TO ANALYSIS OF INSECT IMPACT. J. Forestry 67: 300-304.

Williams, C. B., Jr. and G. S. Walton
1968. EFFECTS OF NALED AND ZECTRAN ON THE BUDWORM, CHORISTONEURA FUMIFERANAE AND ASSOCIATED INSECTS IN MONTANA. J. Econ. Entomol. 61(3): 784-787.

Williams, C. B., Jr. and G. S. Walton and C. F. Tiernan
1969. ZECTRAN AND NALED AFFECT INCIDENCE OF PARASITISM OF THE BUDWORM CHORISTONEURA OCCIDENTALIS IN MONTANA. J. Econ. Entomol. 62(2): 310-312.

Wright, B. S.
1960. WOODCOCK REPRODUCTION IN DDT-SPRAYED AREAS OF NEW BRUNSWICK. J. Wildlife Manage. 24(4): 419-420.

Wygant, N. D.
1959. BARK BEETLE CONTROL. J. Forestry 57:274-277.

■

INTEGRATED CONTROL, PEST MANAGEMENT, OR PROTECTIVE POPULATION MANAGEMENT?

by R. W. STARK, University of California, Berkeley, California (now at University of Idaho, Moscow, Idaho).

THE PREOCCUPATION of foresters and forest entomologists in suppressing populations of phytophagous insects competing for the forest resource has led to the establishment of several "territories":

Mechanical control.—Mechanical methods such as burning or felling, and peeling and burning the bark of trees infested by bark beetles.

Chemical control.—Applying insecticides.

Biological control.—Utilizing predators, parasites, and diseases. Classical biological control emphasized the use of introduced parasites, predators, and diseases for exotic insects.

Silvicultural control.—Utilizing silvicultural and management practices.

Ecological control.—Includes not only biological and silvicultural methods but also selection of genetically resistant trees.

To this list should be added the new definition of biological control. Biological control now encompasses all methods of control that can be considered biological in nature—excluding chemical and mechanical.

Two more definitions of control came into being more or less simultaneously: harmonious (*Voute 1964*) and integrated (*Smith and Allen 1954*; *Stern et al. 1959*). Both were a consortium of territories.

Harmonious control.—A synthesis of ecological, chemical, and eventually mechanical. It includes integrated control. It is the

most many-sided idea of control of insect pests possible. The application of pesticides is not abandoned, but is intended for use in addition to other methods since it is explicitly stated that chemicals should not interfere with natural population regulators.

Two definitions of integrated control are necessary, first to establish proper priority, and second to define its current status.

Integrated control.—The earliest definition of integrated control (*Smith and Allen 1954*) recognized the necessity for consideration of the ecosystem; but social, political, and economic pressures necessitated an immediate reconciliation between chemical and biological control. The definition arrived at by Stern *et al.* (*1959*) was more palatable at the time to growers and industry. This was: "applied pest control which combines and integrates biological and chemical control." As techniques improved, the benefits of minimizing pesticide use became more apparent, and the hazards of intensive use of chemicals more obvious; and the broader concept of integrated control evolved.

Smith (*1969a, b*) said: "Integrated control is a pest population management system that, in the context of the associated environment and the population dynamics of the pest species, utilizes all suitable techniques and methods in as compatible a manner as possible and maintains the pest populations at levels below those causing economic injury."
and, further:

"Integrated control is an ecological approach to the control of harmful pests. It derives its uniqueness from emphasis on the fullest practical utilization of existing mortality and suppressive factors in the environment. Its strategy is one of 'management and containment' rather than 'seek and destroy.' The goal of the integrated control system is to provide a stable and economically sound procedure for crop protection."

There are two principles common to both these definitions, but particularly the later one, without which the definitions are incomplete. These are: (1) consider the ecosystem, particularly avoiding disruptive actions, and (2) utilize critical injury levels.

By agreement, at various international symposia, integrated

control is used in appropriate literature rather than harmonious control. I think it is obvious at this stage that there is a drawing together of ideas concerning pest regulation.

The concept of utilizing natural enemies and forest cultural methods to minimize damage by forest insects is deeply rooted in European forestry (*Voute 1964*). Those chemicals used were natural compounds, and biologists were more or less forced to study natural causes and treat accordingly. When broad-spectrum insecticides appeared they were utilized but with far more respect for the environment than in North America. The store of fundamental knowledge built up over the centuries in the care of their forests was not neglected as it has been in North America. Verbal formulation of the concept of harmonious control began about 1958.

In North America, faced with a superabundance of forest resources, early foresters were little concerned with the relatively minor losses inflicted by forest insects or diseases. It was not until late in the 19th or early in the 20th century, when large capital investments in physical plants were made, that losses in the vicinity of those industries became of concern. Then the myth of superabundance was replaced by the myth of supertechnology, encouraged by the apparent success of lethal insecticides in agriculture. Initial apparent successes in "pest control" led to what Graham (*1964*) refers to as "preoccupation with procedural aspects". A type procedure was adopted for each situation as it arose, and the underlying manipulations were largely ignored.

Meanwhile, the agriculturists were learning that the use of a single kind of control procedure was not solving the problem. Indeed, new and more serious problems were evolving, and integrated control in its narrow sense evolved (*DeBach 1951*); *Griffiths 1951; Pepper 1955; Pickett et al. 1958; Ripper 1944, 1951; Smith and Hagen 1959; Stern et al. 1959*). Although most ecologists and entomologists had long embraced the ecological approach to pest regulation, it was not until evidence accumulated on the harmful side effects of pesticides and public reaction and opposition to their use increased, that the broader and more inclusive concept began to be promulgated and accepted

(*Chant 1966a; FAO 1966, 1968; Geier and Clark 1960; Smith 1963, 1968a, 1969a; Smith and Reynolds 1965*).

The concept of integrated (harmonious) control grew out of forestry practices in Europe and agriculture in North America. There have been to date only token efforts to apply the system in forestry. Early forest entomologists and biologists preached the lessons learned from European foresters, but their sermons fell largely on deaf ears. If one goes to texts of S. A. Graham, Hawley and Stickel, and others he will find the seeds of the "integrated control" concept planted there. They are only now beginning to show signs of germinating. Smith (*1963*) and Franz (*1965*) are among the most recent to propose that we fertilize them.

However, the situation is still in a state of flux. Several recent authors have proposed another way of looking at this whole problem of protecting our forest resource from its enemies. Since the forestry profession, as I see it, is on the brink of embracing something along this line, I think it behooves us to examine this concept. We may not have to tread in every footstep the agriculturists have placed before us—perhaps we can skip a few. I refer, of course, to the concept of "pest management", or "protective population management".

Geier and Clark (*1960*) coined the term "protective population management". They argued that a continuous sequence of ad hoc programs of destruction of noxious insects has occupied available personnel so that they have ignored fundamentals of ecology, including socio-economics—which is really ecology. In practice, there is no real difference between their definition of pest population management and integrated control. Geier (*1966*) shortened the name to "pest management" and stated:

> [it] was coined to emphasize the comprehensive nature of the approach and to underline its preoccupation with ecological realities. It is intended to convey the idea of intelligent manipulation of nature for man's lasting benefit. The greatest single quality which the new strategy should possess is selectiveness in its action on a specific population. This selective action must remain at all times commensurate with population's potential injuriousness. To achieve that, the new approach must aim, above all, at making control operations fit well with the biology of the noxious species.

It should be noted that in a truly ecological sense no manipulation of the environment is truly selective. Beirne (*1967*) broadened the concept of pest management:

> Pest management is one of a number of more or less analogous terms that refer to management of aspects of the environment in ways that will benefit our interests . . . [It] refers to actions at a different level, actions that are primarily aimed at harming living organisms that are harmful to us or to resources that we use. . . It consists of the intelligent management of pests and of their surroundings and the management of the people who devise or do that managing. The management of pests is commonly what is meant by the term pest control.

Authors have in recent years begun to use the terms pest management and integrated control interchangeably. For example, the index of recent publication of the National Academy of Sciences "Insect Pest Management and Control" (*1969*) has the curious section heading "Successful Unilateral Pest-Management Systems".

Chant (*1966b*) suggested that pest management and integrated control are synonymous. Smith (*1968b*) used the term pest management almost exclusively when discussing the ecological approach to pest regulation and mentioned the social and political ramifications. However, although the rationale of both are practically identical and the guidelines for integrated control (*FAO 1968*) can be incorporated as a part of the guidelines for pest managers, I feel we should consider pest management and integrated control as two distinct entities. Pest management should be considered as a component of resource management (*Watt 1968*). Integrated control is the approach by which regulation of pest populations is achieved, whereas pest management is the decision-making process where all aspects such as societal values, impact on other resources, and the like are considered prior to making the decision whether population regulation is to be undertaken.

Management of Pests

One of the fundamental principles of integrated control can be transposed intact to pest management: "utilize critical injury levels" (*Smith 1969a*). This has been variously named economic

threshold (*Stern et al. 1959*), action threshold (*Chant 1966a*), and economic injury level. The intent is clear, but the application in practice is not simple and requires examination in the forest environment.

The concept of economic threshold as developed for agricultural entomology is not adequate for most decisions in management of forest pests. It was developed along strict profit-loss relationships and does not include sufficient recognition of forest ownership and mixed values.

There are approximately 773,400,000 acres of forested land in the United States, 461,044,000 of which are classed as commercial. If an insect problem occurs on the noncommercial forested land, how do the economic considerations of marketplace values on which most of our evaluations are based apply? Of the commercial forested land, approximately 106,071,000 acres are under public guardianship, either federal, state, or other. Portions of this land are designated as national forests, national parks, wilderness areas, and other types of reserves, administered by a variety of agencies. Again, how do you apply *economic* thresholds compatible with the multitude of uses involved? Of the remaining commercial land, about 350 million acres, an estimated 59 percent, is in scattered nonindustrial private holdings that are either not managed at all or only slightly so. How can you apply *economic* thresholds to land that is not managed for its crop? The economic threshold is defined as the density (of the pest population) at which control measures should be determined to prevent an increasing pest population from reaching the economic injury level. The economic injury level is the lowest population density that will cause economic damage (*Stern et al. 1959*). Use of this concept is, at best, feasible only for that 150 million acres under management for forest crops.

Johnson (*1963, 1966*) and others have addressed themselves to the problem of determining economic thresholds under various commercial forest situations and have pointed out that even where a single ownership is involved and the kind of crop is fixed, the task of determining the benefits derived may be far from simple. A forest crop such as a nursery or a Christmas

tree plantation approaches the agricultural situation, and the techniques of establishing economic thresholds can be applied with justification. But if the crop depends on a harvest 80 years from the time of planting, how can you apply today's marketplace values and control costs to a product (for example, lumber) that not only fluctuates markedly in value for top-grade products but just as widely depending on the quality?

In most commercial situations in forestry the "economic thresholds," where they are set at all, are set arbitrarily and are dictated largely by emotional responses—fear of what might occur rather than any justified economic base. The many absurd "control projects" committed in the name of protection are possible only through government subsidy. Outbreaks that truly jeopardize commercial managed forests are rare even in apparently susceptible uniform forest types: where they occur they rarely proceed unchecked to eliminate entire forests. The chief malefactors, bark beetles, although they may cause cessation of growth (death) of significant portions of the stand, do not destroy the crop. It remains there, amenable to harvest, should the management plan be flexible enough to utilize it (*Johnson 1940*). Also, much of our forest economy is geared to a single product. Where the product is only lumber, a dead tree, blue-stained and invaded by secondary insects, may be a total loss; but in a multiple-use industry, most of the tree may be recoverable.

The emotional response to insect kill and damage is often unrealistic, as is the attitude that we must give away, in the name of control, perfectly valuable ponderosa pine, Douglas-fir, sugar-pine, etc., killed by bark beetles. Occasionally, as in catastrophic storms with the incipient insect consequences, this may be justified; but the annual sales of bug-killed trees and adjacent green (infested or not) timber at prices far below going prices and additional tax benefits seems to me questionable.

It is not unlike the situation existing in the cotton industry. Annually the Government spends millions of dollars for landowners *not* to grow cotton. At the same time, research agencies, growers, and the Government spend millions to protect what cotton is grown! It would seem to me that if a national policy

were developed that would permit rotation of crops over the total range of cotton land, a balance might be achieved with cotton plants, insects, and national production goals. If restricted to cotton lands, subsidiary industries would not suffer unduly as it is unlikely that in any particular area no crops could be grown. For those growers who could demonstrate a financial loss from changing to another crop, an indemnity replacing the no-grow subsidy would suffice.

Another example of abuse of the economic threshold concept is the spruce budworm problem in eastern Canada. The vast acreages over which control has been attempted often have little relation to the economic interests involved. The areas covered by such control, and this applies to budworm control in Montana and Washington as well, if on commercial land at all, usually exceed any that might conceivably be utilized in a lifetime. There would be ample time for a replacement crop to mature—assuming the budworm did its worst. Protection of a national resource is then invoked. A type procedure—chemical spraying—is adopted, and a private corporation is formed to carry out this procedure. This would seem to be the acme of "Graham's Law" (*1964*), to the end that once a type procedure is adopted for a type situation it is pursued inflexibly without thought of what it is actually contributing. The dissolution of a public corporation or a government bureau because of obsolescence is a difficult feat to accomplish!

Many authors have stated that we do not have realistic estimates of the impact of insects in forests upon which to base treatment decisions. There is confusion between injury and damage (*Smith 1968c; Strickland and Bardner 1969*). Injury consists of the actual acts of insects, which cause damage to the plant. This damage varies according to insect numbers and behavior. Plant damage is the effect on the plant of the insect injury and may or may not result in crop loss (e.g., beneficial thinning by bark beetles may actually increase yield). Damage may take several forms, such as loss of growth, direct mortality, reduction in quality, and destruction or deterioration of finished products. This determination of realistic estimates of damage is the most urgent item in forest pest management today. I

suspect that we will find that we have little justification for most of the past and existing control programs—at least in the manner in which they are executed.

In an industrial situation it is apparent that the benefits from specific pest-control actions should exceed by an adequate profit margin the total costs of such actions. This cost-benefit ratio should include long-range costs such as costs of treating secondary pest outbreaks, costs of sorting or handling the final product, and supervisory charges. Agriculture, in general, ignores long-range costs—but foresters cannot. The long-range costs or even reasonable estimates of them are usually not available at the time the decision must be made. Unfortunately also, the decision-maker, even if aware of them, may feel that the long-range costs need not be accounted for by him, but will be paid for by the succeeding generations or a remote government or society. Hence, unfortunately, most control decisions at the individual producer level are made on a very short-term basis and at current market values. Since in forestry situations insect control is heavily subsidized by the Federal and state governments and decisions usually rest with them, it would seem that this would be amenable to change.

I repeat that the necessity for taking a hard look at our justifications for control is our most urgent task, and it has always been a matter of wonder to me (and lately slightly of suspicion) why forest economists have, in general, ignored this problem. I think the techniques for developing economic criteria for at least industrial forest lands are available. I believe the use of the life-table approach adapted by Waters (*1969*) married to the systems-analysis techniques of Amidon (*1966*), Hill and Amidon (*1968*) and Davis (*1968*) with existing data will provide realistic figures in industry-oriented forests for those forest insects currently considered pests. What is required is that a pest manager and a forest manager integrate their respective resources and talents to that end.

To this point I have limited this discussion of "economic threshold" to industrial forest land, essentially "cost-benefit" relationships. The greatest bulk of forested land is not in "production" in the strict sense, and although I do not have fig-

ures, I would hazard a guess that as many control efforts are on this public land as are on private. The criteria for control decisions on public land dedicated to various uses is infinitely more complex than on industrial land.

The most comprehensive example of the problems involved is given by Vaux (*1954*), who discussed the economic implications of a vast control project involving the outbreak of Engelmann spruce beetle in Colorado. The justifications invoked (and which are commonly invoked by forest entomologists) were protection of watershed values, recreation values, and timber utilization. Assigning economic values to the first two is an exercise in frustration. It may never be possible.

Rather than attempt to commercialize what are essentially sociopolitical problems, why can we not assign "critical injury limits" based on a risk-benefit ratio (*Starr 1969*) where the risk to that particular enterprise is evaluated not in dollars but in relation to its continued efficiency in that particular function? For example, the most efficient watershed is probably paved so there is no loss by transpiration and interception. The water is conveyed immediately to covered storage ponds in the valleys, and runoff is regulated by valves. Although not well documented (which means I could not find any references), the belief exists and is growing that heavy forest (tree) cover is not particularly efficient in terms of water production. Perhaps insect kill or heavy defoliation may actually be beneficial in terms of water supply. Additional risks to be considered, however, would be increased fire hazard, increasing protection costs, and perhaps less efficient flood control.

Some economic values can be assigned to recreation—for example, fishing and hunting permits, increased number of tourists, average dollars spent, etc.—but these so overlap and depend upon so many intangible values that to assign the value to the forest or lack of it alone would be misleading if not false. Does the presence of extensive budworm defoliation or beetle kill really affect recreation possibilities? Does it really discourage people from visiting forested areas? My experience in Canadian and Californian national parks indicates that if such damage has any effect, it is negligible. In fact, in Yosemite Na-

tional Park, the Ghost Forests of Tioga created by a needle miner outbreak is an attraction!

The spruce bark beetle outbreak was mentioned above. According to Vaux (*1954*), a separate economic analysis of the area indicated that the timber area affected constituted a poor investment risk. The appearance of the area affected, including untreated areas that have undergone extensive beetle outbreaks in Canada and California lead me to state that apparently such outbreaks created no material effect on watershed or recreation. What is required in pest management is an extremely broad perspective in assessing risk from outbreaks on noncommercial lands. The pest manager must look at the area from at least a regional view, if not national. Consideration of land allocation must be included. For example, the Rocky Mountain States are the least productive part of the United States for timber production (*Wagar 1969*). Northern Idaho and western Montana already have more industrial plant capacity than can be kept supplied with current levels of timber management. Old-growth stands once permitted (without management) a profitable industry, but this is not true today. This has created a pressure to permit use of old-growth stands locked up in national forests. Whether this comes to pass or not, it merely prolongs the situation. On the other hand, these same areas are extremely rich in watershed and potential power sources for the Northwest and Central States and in recreation potential. My point is that the pest manager, in concert with the forest manager, should examine land use in this context.

One last example of the necessity for broadening the scope of pest management to be included in the resource-management level is closer to home. The research forest of the University of California is located in a highly productive mixed conifer forest. A recent study (*Teegarden and Werner 1968*) presented a case history of integrating forest-oriented recreation with timber growing. They pointed out that under certain conditions conversion of timberland to vacation homesites was a profitable venture. Lacking in their analysis was consideration of costs for protection from bark beetles. Since bark beetles are a chronic problem in the area studied, and since protection costs in vaca-

tion home areas far exceed those in commercial forests, consideration of this may well affect such decisions. On the other hand, an area identified as a focus of bark beetle populations was determined to be unproductive from an economic point of view. The ends of pest management and land use would both be met if such areas were removed from timber production, which is under constant threat from insect damage, and converted to other uses such as vacation homes, grazing meadows, or recreational areas if suitably located.

The second basic principle of integrated control—"consider the ecosystem"—is of particular importance in the forest environment. The forest ecosystem as implied above is much more diverse than most agricultural ecosystems. Public ownership of and public concern for the forests far exceeds that of any agroecosystem. Our values are many and diverse, and the pest manager must be cognizant of these and include them in his recommendations.

The conventional approach to methods of control is oriented toward procedures or classes of procedure (chemical control, biological control, etc.) and to date, never set forth in an integrated system. None of the classifications of forest insect control differentiate clearly between the ramifications of a course of action and the underlying ecological theory to be served. We are sadly deficient in our understanding of the forest ecosystem, but this lack is being rectified. It seems to me that the tremendous economic growth of forestry in the past has blinded us to the fact that prior to our exploitation of the forests, forest pest problems were much less. In many of those areas that are still relatively undisturbed, problems are usually minimal. Why? It is apparent that the great majority of phytophagous insects never reach outbreak levels, and their numbers fluctuate far below the capacity of food plants to support them. Whatever theory of population regulation you ascribe to, the fact remains that the majority of our pests are man-made. It seems to me that the forests, because of their inherent species diversity (both floral and faunal) and the relatively long time over which they develop, lend themselves to the ecological approach to pest regulation and, conversely, are more susceptible to upset by a

strictly unilateral approach. We should have learned earlier from the agricultural entomologists that rarely, if ever, will single factor treatment, such as the use of parasites, predators, diseases, or an insecticide, achieve true regulation of insect populations.

Forest entomologists have, to a considerable degree, been guilty of parochialism in their approach to the problem. They have sought explanation of the eruption in entomological terms rather than ecological. On the other hand, forest entomologists have been responsible for major advances in ecological theory. However, now more than ever, it is essential that we approach each problem insect from a truly ecological viewpoint. The evidence is accumulating that outbreaks of forest insects are symptomatic of ecological disturbances in the forest ecosystems. We now have examples of insect problems occurring as a result of air pollution (*Sinclair 1969*), root diseases (*Stark and Cobb 1969*), possibly excess organic debris, site effects (*Fauss and Pierie 1969*; *Bess et al. 1949*), and probably infection by nematodes (*Ruehle 1969*) as well as the many well-documented causes (*Graham 1963; Graham and Knight, 1965*).

Yet these problems, many known for a long time, have been much less the object of study than the application of insecticides. To effect forest pest management we must investigate the true cause of insect population fluctuations and determine ways of rectifying the underlying problem. This may not be completely feasible, and regulation may be necessary. Regulation may also be necessary while attempting to determine the cause and rectify it, and the ecological approach to population regulation—integrated control—should be our goal. The pest manager should be dedicated to consider all potential techniques relevant to the particular problem, while remaining obedient to practical realities. We are obsessed when faced with an apparent abundance of insects that we *must do* something. Perhaps doing nothing might be the right decision.

We should be aware that many of our problems have their parallel in forest pathology, and the pest manager should not restrict himself. To illustrate this I have selected a few statements from books and papers in forest pathology and forest en-

tomology. I will not identify them or elaborate on them. The message should be obvious.

X	Y
Trees growing on good sites . . . are more vigorous than those on poor sites.	Vigorous trees survived when growing on favorable sites whereas less vigorous trees in same localities did not.
Trees growing under optimum stocking conditions according to age and size are more vigorous than those that are overmature.	The destruction may be reduced by regulation of forest density.
Trees from sapling age to physiological maturity are more vigorous than those that are overmature.	The importance of loss and the irreversible effects of damage increase with the age of the problem.
Uninjured trees are more vigorous than those that have had to withstand injurious influence.	Scarring of trees during logging increases incidence of the problem.

I have tried to convey the concept that, in our task of preventing damage to the forest ecosystem (whatever our value system), we should avoid the trap of merely adopting a new procedural philosophy, i.e., integrated control as a set of techniques. Rather, either individually or in cooperation with others of our persuasion and the resource manager, we look at the entire ecosystem from the viewpoint of resource management in the broadest sense.

Conclusions

Pest management, implied in the use of the human-oriented word pest, deals with the real world. Many of us have a tend-

ency to turn away from a real and immediate problem and approach it from so fundamental a level that we never get back to the problem in time to join in the solution of it.

On the other hand, we tend to think of population oscillation as being made to happen, and we seek that factor that caused it. We ignore the possibility that events happen because some antecedent event, by not happening, failed to prevent that particular oscillation. This may require extremely fundamental work.

This pest manager is an individual who has the ability to consider all variables simultaneously, is sensitive to feedback from tentative calculations, application results, and environmental or social reaction, whatever the source, is capable of assessing strategies for the deployment of time and resources, and is able to perceive the relevance of one fact to another or of hypothesis to fact (*Caws 1969*).

Also, the pest manager should bring together all elements of protection and should be subject to dictates of the forest resource involved. The forest manager should bring together all the potential uses and benefits of the area in question. Man is an animal with ingrained territorial instincts, so we tend to view the forest from our particular territory; for example, lumber producing, fishing area, a place for privacy, etc. Many forests are capable of being almost all things to all people and should be so viewed. The final set of values decided upon for any particular forest or region has a profound influence on pest management decisions.

Forest pest management can be viewed in three stages (*Geier and Clark 1960*).

1. Treatments should no longer be applied blindly according to type procedures inherited from the past or other disciplines, but should be made to conform objectively with the forest ecosystem, local circumstances, and the future.
2. A working knowledge of the natural numerical regulation of noxious species and particularly the identification of existing limiting density factors must be acquired. Regulation of an insect population should be viewed as an exercise in population dynamics.

3. Suppression of intolerable population levels (whatever the criterion) is the ultimate consequence of comprehensive husbandry based on sound ecological fact and theory. The integrated control concept is the embodiment of this philosophy.

Although great creative effort will be necessary, stage 3 should prove to be less costly, invoke less social and ecological repercussions, and be of more lasting benefit than the continued use of present-day methods, which ignore the ecological realities of pest regulation.

Last, I would like to quote the Society of American Foresters policy statement concerning forest protection. Although more honored in the breach than in observance, the philosophy of pest management is contained there:

> Protection commensurate with the values protected is essential to the management of all forest land resources. The Society advocates coordinated, intensive efforts to reduce and prevent forest losses from fire, insects, diseases, animals and other causes. Cooperation among all protection organizations and forest landowners will best achieve the objectives. Prevention is the ideal form of protection and is furthered through strong information and education programs. Public and private forest owners and the general public share the responsibility and benefits of adequate forest protection. The Society endorses programs of integrated protection involving judicious uses of ecological, biological, chemical and mechanical control."

Let us take heed!

References

Amidon, E. L.
1966. MIADS Z . . . AN ALPHA NUMERIC MAP INFORMATION ASSEMBLY AND DISPLAY SYSTEM FOR A LARGE COMPUTER. USDA Forest Serv. Res. Paper PSW-38, 12 pp.

Beirne, B. P.
1967. PEST MANAGEMENT. 123 pp. Leonard Hill, London.

Bess, H. A., S. H. Spurr and E. W. Littlefield
1949. FOREST SITE CONDITIONS AND THE GYPSY MOTH. Harvard Forest Bull. 22, 56 pp.

Caws, Peter.
1969. THE STRUCTURE OF DISCOVERY. Sci. 166: 1375-1380.

Chant, D. A.
1966a. RESEARCH NEED FOR INTEGRAL CONTROL. FAO Symp. Integrated Pest Contr. Proc. (1965) 3: 103-109.

Chant, D. A.
1966b. INTEGRATED CONTROL SYSTEMS. SCIENTIFIC ASPECTS OF PEST CONTROL. Nat. Acad. Sci. Nat. Res. Council Pub. 1402: 193-218.

Davis, J. B.
1968. WHY NOT PERT YOUR NEXT RESOURCE MANAGEMENT PROBLEM? J. Forestry 66: 405-408.

DeBach. P.
1951. THE NECESSITY FOR AN ECOLOGICAL APPROACH TO PEST CONTROL ON CITRUS IN CALIFORNIA. J. Econ. Entomol. 44: 443-447.

FAO, United Nations
1966. FAO SYMP. INTEGRATED PEST CONTR. Proc. 1965. Rome, Italy, Oct. 11-15, 1965, 3 parts.

FAO, United Nations
1968. REPORT OF THE SECOND SESSION OF THE FAO PANEL OF EXPERTS ON INTEGRATED PEST CONTROL. Rome, Italy, Sept. 19-24, 48 pp.

Fauss, D. L. and W. R. Pierie
1969. STAND CONDITIONS AND SPRUCE BUDWORM DAMAGE IN A WESTERN MONTANA FOREST. J. Forestry 67: 321-325.

Franz, J.
1966. INTEGRATED CONTROL OF FOREST PESTS. FAO Symp. Integrated Pest Contr. Proc. (1956)3: 65-76.

Geier, P. W.
1966. MANAGEMENT OF INSECT PESTS. Ann. Rev. Entomol. 11: 471-490.

Geier, R. W. and L. R. Clark
1960. AN ECOLOGICAL APPROACH TO PEST CONTROL. Symposium 8th Technical Mfg. Int. Union for Cons. of Nature and Nat'l. Res., Warsaw, E. J. Breul, Leiden, pp. 10-18.

Graham, K.
1963. CONCEPTS OF FOREST ENTOMOLOGY. 388 pp. Reinhold, Pa.

Graham, K.
1964. STRATEGY VERSUS TACTICS IN FOREST INSECT CONTROL. J. Forestry 62: 795-798.

Graham, S. A. and F. B. Knight
1965. PRINCIPLES OF FOREST ENTOMOLOGY. 4th ed., 417 pp. McGraw Hill, New York.

Griffiths, J. T.
1951. POSSIBILITIES FOR BETTER CITRUS CONTROL THROUGH THE STUDY OF THE ECOLOGICAL EFFECTS OF SPRAY PROGRAMS. J. Econ. Entomol. 44: 464-468.

Hill, M. R. and E. R. Amidon
1968. INVENTORYING NATIONAL FOREST RESOURCES FOR PLANNING-PROGRAMMING BUDGETING SYSTEM. USDA Forest Serv. Res. Note PSW-178.

Johnson, N. E.
1963. SOME ECONOMIC CONSIDERATION IN PLANNING CONTROL OF INSECTS AFFECTING YOUNG FOREST TREES. J. Forestry 61: 426-429.

Johnson, N. E.
1966. THE ECONOMIC ASPECTS OF FOREST ENTOMOLOGY AND THE FOREST MANAGER. Soc. Amer. Foresters Proc. 1966: 171-174.

Johnson, P. C.
1940. ENTOMOLOGICAL CONSIDERATIONS IN UTILIZATION OF INSECT-KILLED PONDEROSA PINE. J. Econ. Entomol. 33: 773-776.

National Academy of Sciences
1969. INSECT-PEST MANAGEMENT AND CONTROL. Principles of Plant and Animal Pest Contr. Vol 3, 508 pp.

Pepper, T. H.
1955. THE ECOLOGICAL APPROACH TO MANAGEMENT OF INSECT POPULA-

TIONS J. Econ. Entomol. 48: 451-456.

Pickett, A. D., W. L. Putnam and E. J. DeRoux
1958. PROGRESS IN HARMONIZING BIOLOGICAL AND CHEMICAL CONTROL IN ORCHARD PESTS IN EASTERN CANADA. 10th Int. Congr. Ent. 3: 169-174.

Ripper, W. E.
1944. BIOLOGICAL CONTROL AS A SUPPLEMENT TO CHEMICAL CONTROL OF INSECT PESTS. Nature 153: 448-452.

Ripper, W. E.
1951. BIOLOGICAL CONTROL OF CERTAIN COTTON INSECTS AND THE APPLICATION OF NEW ORGANIC INSECTICIDES IN PERU. J. Econ. Entomol. 44: 13-18.

Ruehle, J .C.
1969. FOREST NEMATOLOGY—A NEW FIELD OF BIOLOGICAL RESEARCH. J. Forestry 67: 316-320.

Sinclair, W. A.
1969. POLLUTED AIR: POTENT NEW SELECTIVE FORCE IN FORESTS. J. Forestry 67: 305-309.

Smith, R. F.
1963. INTEGRATED CONTROL—AN APPROACH TO PEST PROBLEMS. Western Forestry & Conserv. Assoc. Luncheon Address, Dec. 10, San Francisco, California.

Smith, R. F.
1968a. RECENT DEVELOPMENTS IN INTEGRATED CONTROL. 4th British Insecticide and Fungicide Conf. Rep. (1967) 2: 464-471.

Smith, R. F.
1968b. THE NEW AND THE OLD IN PEST CONTROL. PROC. OF THE MEETING OF THE ACCADEMIA DEI LINCEI, SEPT. 1968. [In press.]

Smith, R. F.
1968c. PRINCIPLES OF MEASUREMENT OF CROP LOSSES CAUSED BY INSECTS. FAO Symp. Crop Losses. Rome, Oct. 2-6, pp. 205-224.

Smith, R. F.
1969a. INTEGRATED CONTROL OF INSECTS—A CHALLENGE FOR SCIENTISTS. Agr. Sci. Rev. 7(1): 1-5.

Smith, R. F.
1969b. THE IMPORTANCE OF ECONOMIC INJURY LEVELS IN THE DEVELOPMENT OF INTERGATED PEST CONTROL PROGRAMS. Qual. Plant. Mater. Veget. 17 2: 81-92.

Smith, R. F. and W. W. Allen
1954. INSECT CONTROL AND THE BALANCE OF NATURE. Sci. Amer. 190: 38-42.

Smith, R. F. and K. S. Hagen
1959. INTEGRATED CONTROL PROGRAMS IN THE FUTURE OF BIOLOGICAL CONTROL. J. Econ. Entomol. 52: 1106-1108.

Smith, R. F. and H. T. Reynolds
1965. PRINCIPLES, DEFINITIONS AND SCOPE OF INTEGRATED PEST CONTROL. FAO Sym. Integrated Pest Contr. Proc. (1965) 1: 11-18.

Stark, R. W. and F. W. Cobb, Jr.
1969. SMOG, INJURY, ROOT DISEASES AND BARK BEETLE DAMAGE IN PONDEROSA PINE. Calif. Agr. 23(9): 13-15.

Starr, Chauncey
1969. SOCIAL BENEFIT VERSUS TECHNOLOGICAL RISK. Sci. 165: 1232-1238.

Stern, V. M., R. F. Smith , R. van den Bosch and K. S. Hagen
1959. THE INTEGRATION OF CHEMICAL AND BIOLOGICAL CONTROL OF THE SPOTTED ALFALFA APHID. PART I. THE INTEGRATED CONTROL CONCEPT. Hilgardia 29: 81-101.

Strickland, A. H. and R. Bardner
1968. A REVIEW OF CURRENT METHODS APPLICABLE TO MEASURING CROP LOSSES DUE TO INSECTS. FAO Symp. Crop Losses. Oct. 2-6, 1967, pp. 289-309.

Teegarden, D. E. and K. R. Werner
1968. INTEGRATING FOREST-ORIENTED RECREATION WITH TIMBER GROWING. Calif. Agr. 22(10): 10-13.

Vaux, H. J.
1954. SOME IMPLICATIONS OF THE SPRUCE BEETLE CONTROL AND SALVAGE PROGRAMS IN COLORADO. J. Forestry 52: 506-510.

Voute, A. D.
1964. HARMONIOUS CONTROL OF FOREST INSECTS. Int. Rev. Forestry Res. 1: 325-383.

Wagar, J. Alan
1969. NON-CONSUMPTIVE USES OF THE CONIFEROUS FOREST, WITH SPECIAL RELATION TO CONSUMPTIVE USES. Univ. of Montana Foundation, Coniferous forests of the northern Rocky Mountains Symp. 1968: 255-270.

Waters, W. E.
1969. THE LIFE TABLE APPROACH TO ANALYSIS OF INSECT IMPACT. J. Forestry 67: 300-304.

Watt, K. E. F. (ed.)
1966. SYSTEMS ANALYSIS IN ECOLOGY. 776 pp. Acad. Press. New York.

Watt, K. E. F.
1968. ECOLOGY AND RESOURCE MANAGEMENT. 450 pp. McGraw-Hill, New York.

■

THE FOREST SERVICE of the U. S. Department of Agriculture is dedicated to the principle of multiple use management of the Nation's forest resources for sustained yields of wood, water, forage, wildlife, and recreation. Through forestry research, cooperation with the States and private forest owners, and management of the National Forests and National Grasslands, it strives — as directed by Congress — to provide increasingly greater service to a growing Nation.