THE EQUILIBRIUM STRUCTURE AND BEHAVIOR OF DEFOLIATING INSECT SYSTEMS

by

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We accept this thesis as conforming to the required standard

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Defoliating insect systems, defined for the purposes of this thesis as being composed of insects which defoliate forest trees and the species with which they interact, such as their host trees and their natural enemy complexes, exhibit a wide variety of population behaviors. Similarly, a number of theories and models have been proposed to explain these behaviors. These theories emphasize the importance of different ecological processes, often concentrate on the defoliator and overlook the importance of other components. Also, much of the current understanding of the dynamics of these systems has come from forest pest research and management programs, tailored towards specific pest problems and often very short term in nature.

This thesis develops and begins to test a general approach for the local dynamics of defoliating insect systems. This framework outlines the system components that are necessary to predict the behavior of defoliating insect systems. It includes ways in which the equilibrium structure of defoliating insect systems, defined as the number of equilibria for each system component, the population levels at which the equilibria occur, and the processes creating the equilibria, might be found. The framework also includes methods of inducing the qualitative behavior of these sys-
tems, defined as the periodicity of defoliator outbreaks, the length of outbreaks, and the dynamics of other important system components between, during, and in the decline of defoliator outbreaks.

The study begins with a detailed literature review of historical theories of defoliating insect system behavior and of the documented behavior patterns of these systems. Major classes of behavior are identified, as well as the various ecological processes which have been invoked to explain these behaviors. An analysis and documentation of the equilibrium structure and behavior of three defoliating defoliating insect systems, the eastern blackheaded budworm, the eastern spruce budworm, and the jack pine sawfly, are then used to develop general rules about how equilibrium structure and behavior can be explained. This analysis, coupled with the literature review, is used to develop the framework. The framework is then tested against historical defoliator population data and general syntheses of defoliating insect system research to assess its utility and predictability.

The major results of the thesis are as follows. First, it appears that the structure and behavior of a defoliating insect system can be explained with five dynamic variables: the abundances of the defoliator; the foliage; the forest; the parasitoid; and the disease; and the effects of weather acting on the defoliator. Second, there appear to be 4 classes of defoliating insect system behavior. Third, the
behavior that a defoliating insect system will exhibit seems to be determined by the magnitude of weather effects on defoliator survival and recruitment, the parasitoid numerical response to changing defoliator densities, the disease numerical response to changing defoliator densities, and the vulnerability of the forest to defoliation. Fourth, there seem to be four equilibrium structures the defoliator can exhibit, and one each for the parasitoid, the foliage, the forest, and the disease. Finally, the framework suggests that defoliating insect system structure and behavior can be induced with a particular, well-defined set of information.

The framework is successful when applied to particular defoliating insect systems for explaining their behavior, but less successful in explaining defoliator equilibrium structure for other systems. Opportunities for more thorough testing of the framework exist if the particular types of data outlined above are gathered for defoliating insect systems. This lack of data for testing the framework make it currently difficult to clearly define those systems in which the framework is useful and those systems in which it is not. Experiments to test the framework are described and suggestions for future types of applied research on defoliating insect systems are presented.
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1.0 INTRODUCTION

1.1 Overview

Defoliating insect systems, defined for the purposes of this thesis as being composed of insects which defoliate forest trees and the species with which they interact, such as their host trees and their natural enemy complexes, exhibit a variety of behaviors. In terms of defoliator population dynamics, behavior varies from chronically non-outbreak to long-lasting, infrequent infestations (eastern spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae) Baskerville 1958) to long-lasting, regular outbreaks (jack pine budworm, *Choristoneura pinus* (Lepidoptera: Tortricidae) Canada 1939 to 1982) to regular outbreaks of short duration (Douglas-fir tussock moth, *Orygia pseudotsugata* (Lepidoptera: Lymantriidae) Wickman 1963) to almost perfectly regular oscillations (larch budmoth, *Zeiraphera griseana* (Lepidoptera: Tortricidae) Baltensweiler 1968). Parasitism rates can fluctuate markedly with changing defoliator densities (eastern black-headed budworm, *Acleris variana* (Lepidoptera: Tortricidae) Miller 1966) or fluctuate relatively little (eastern spruce budworm, Miller 1963). Susceptible forests can suffer little or no mortality from infestations (spruce budmoth, *Zeiraphera spp.* (Lepidoptera: Tortricidae) Carrow 1985) or experience extremely heavy mortality (eastern spruce budworm, Baskerville, 1958). A defoliating insect system can exhibit radically different behaviors in different parts of its extent (larch sawfly, *Pristiphora erich-
sonii (Hymenoptera: Tenthredinidae) (Turnock 1972) or at different periods of time (larch sawfly, Turnock 1972, European spruce sawfly, Diprion hercyniae (Hymenoptera: Diprionidae) Neilson and Morris 1964).

Similarly, there are a variety of models of defoliating insect systems (western tent caterpillar, Malacasoma disstria (Lepidoptera: Lasiocampidae) Wellington et al. 1975, Douglas-fir tussock moth, Brookes et al. 1979, eastern spruce budworm, Clark and Holling 1979, larch budmoth, Fischlin and Baltensweiler 1979, eastern black-headed budworm, McNamee 1979, European pine sawfly, Neodiprion serrifer (Hymenoptera: Diprionidae) Wallace and Griffiths, in prep., gypsy moth, Lymantria dispar (Lepidoptera: Lymantridae) McNamee et al. 1983). All these models, to a greater or lesser degree, are articulations of current understanding of the key ecological processes which give rise to the observed dynamics of the systems.

Several features of these models are worth noting. First, different ecological processes have been identified as important in the various cases. For example, Brookes et al. (1979) emphasize the role of a viral disease in causing collapse of Douglas-fir tussock moth infestations, Clark and Holling (1979) describe forest and foliage dynamics as important determinants of eastern spruce budworm system behavior, while Fischlin and Baltensweiler (1979) hypothesize that dispersal and foliage quality regulate the dynamics of larch budmoth populations. Second, the models
tend to concentrate largely on the insects and their population behavior. Features and dynamics of other system components are often overlooked. Third, many of the models were constructed under the auspices of particular forest pest research and management programs, specifically designed to address resources affected by the forest pest. The research programs which have usually accompanied the modeling efforts have been very short term in nature, often being shorter in duration than a complete defoliator population cycle.

The end sum of these historical efforts is a fragmented picture of the dynamics of defoliating insect systems. There is no single, general theory of defoliating insect system behavior which integrates all examples into a common ecological structure. Of course, pest research or management efforts must address specific needs. But, must each defoliating insect system be considered a unique entity, and are we doomed to treat every forest pest system as completely different? I suggest not, based on the following observations.

Work done on the eastern spruce budworm/balsam fir system (Baskerville 1976, Clark and Holling 1979) indicated that qualitative properties of its historical dynamics can be traced to a small set of interactions among a small number of system components, or state variables, each with a different temporal scale, or rate of population turnover, or change (Ludwig, Jones, and Holling 1978, Jones 1977a,b,
McNamee, McLeod, and Holling (1981). These interactions in the budworm system determine the equilibrium structure, or the number and position of population equilibria (Peterman et al. 1979) of the system. Radically different temporal behaviors of the model system occur when the characteristics of those interactions, and therefore their effect on the equilibrium structure, are changed. Some of the different behaviors have been observed in the real world system (Clark and Holling 1979), while some behaviors have not (McLeod 1976a). But, all alternate behaviors occur regularly in other defoliating insect systems.

Also, the effect of many ecological processes on the equilibrium structure of populations is known and predictable (Holling 1959, Takahashi 1964, Southwood and Comins 1976). Therefore, questions concerning the prediction of equilibrium structure can perhaps be reduced to questions concerning the presence or absence and characteristics of a small set of ecological processes.

These observations suggest that the equilibrium structure of key system variables can be predicted by knowing whether a few processes occur in that system and, if they do, knowing their characteristics and rate. Given the equilibrium structure, it may be possible to make some strong predictions about the temporal behavior of the system.

1.2 Objectives
The above observations lead to the objectives of this thesis. Specifically, I wish to begin deriving a general, integrative theory of structure and behavior of defoliating insect systems. The term "integrative theory" means, in this thesis, a theory in which a small number of ecological processes are used to explain the behavior of all defoliating insect systems. This theory will:

1. define a set of components, or state and driving variables which are necessary and sufficient to predict the qualitative properties of defoliating insect system behavior;

2. collapse the plethora of defoliating insect system behaviors into a small set of classes, each identified by characteristic temporal properties of the components;

3. show how the classes of behavior can be induced from a set of key interactions among the components;

4. show that the state components each exhibit one of a small number of different equilibrium structures; and

5. show that the key interactions among the components which determine system behavior and the equilibrium structures of the components in any defoliating insect system can be predicted with a
minimum set of information about the components themselves.

1.3 Bounds of This Thesis

In general, the development of the integrative theory will occur through a consideration of specific processes which have been well-studied in a small number of defoliating insect systems. Therefore, by default, I will be omitting consideration of other processes in the development of the theory. I will present a description of all processes which scientists have felt are important in the dynamics of defoliating insect systems in a review early in the thesis. In addition, the thesis summary chapter will discuss the possible implications of the results of this theory for the importance for some of these other processes.

In particular, I have chosen to concentrate my efforts in this thesis on the development of a general integrative theory for local population dynamics. This thesis will not address the effects of insect dispersal on the behavior of defoliating insect systems and the theory will not predict the spatial dynamics of these systems.

Also, in this thesis, I am only interested in the qualitative behavior of defoliating insect systems. I define qualitative behavior of defoliating insect systems as the period of time between insect outbreaks, the length of insect outbreaks, and the dynamics of other important state
variables between, during, and in the decline of insect outbreaks. This is to distinguish this description of behavior from that of detailed descriptions of year to year changes in abundances of the state variables.

### 1.4 Approach and Organization of This Thesis

The approach I have adopted to meet the objectives outlined above has five major components.

The first component is a detailed literature review which describes the various patterns of qualitative behavior found in defoliating insect systems and presents the various theories historically proposed to account for their behavior. This review will identify the major classes of qualitative defoliating insect system behavior and lay out the various ecological processes which have been invoked to explain this behavior. This will be particularly useful after the integrative theory has been developed to examine exactly what previous theories are integrated, how they have been integrated, and which previous theories remain outside of the integrative theory. The literature review is provided in Chapter 2.

The second component of the approach is a careful analysis and documentation of the equilibrium structure and behavior of simulation models of three of the defoliating insect systems which have been described in the literature review: the eastern spruce budworm, the eastern black-headed budworm, and the jack pine sawfly. An extensive set of
quantitative data has been collected on these three systems and they are or were the subject of research and management programs. This model analysis is provided in Chapters 3 to 5. The methods of model analysis will be provided in the introduction to Chapter 3. These methods involve primarily the use of recruitment and isorecruitment curves for system variables and predator-prey isocline analysis as developed by Rosenzweig and MacArthur (1963).

The third component of the approach is a synthesis of the results of the model analyses and the literature review into an integrative theory of defoliating insect system behavior. I use results from the previous chapters to derive a general set of rules which can be used to predict the temporal behavior of defoliating insect systems with a minimum set of information. This synthesis and description of the integrative theory is provided in Chapter 6.

The fourth component of the approach is an attempt to invalidate of the theory. I examine the predictive capabilities of the integrative theory on the other defoliating insect systems presented in the literature review. This testing is undertaken using long term population records, Forest Insect Survey records of Canada, and extensive scientific summary documents of particular case studies where they exist. I also describe appropriate field experiments which would provide definitive tests of the theory. This is provided in Chapter 7.
The final component of the approach is a critical examination of previous theories of defoliating insect system structure and behavior, presented in Chapter 2, in the light of the results of this thesis and the general integrative theory I have developed. I conclude by examining the implications of my results for defoliating insect research or management programs. This critical review and summary is provided in Chapter 8.
2.1 Introduction

Chapter 1 suggested the importance of both equilibrium structure, and of ecological processes affecting equilibrium structure, in determining temporal behavior of defoliating insect systems. The objectives presented in Chapter 1 also indicated that the integrative theory to be developed would utilize both equilibrium structure and dynamic ecological processes in helping to induce temporal behavior. It is therefore worthwhile to review the documented patterns of defoliating insect system behavior, historical efforts at explaining these behavior, in terms of ecological processes hypothesized to be important and in terms of the equilibrium structure implied by these processes. This review will help to view the work that follows in proper context and allow comparison of the work with previous attempts at explaining the behavior of defoliating insect systems.

This chapter has four specific objectives:

1. present the methods of analysis that will be used in examining historical theories of structure and behavior of defoliating insect systems and in developing the integrative theory;

2. present the evolution of ecological theory pertaining to equilibrium structure;
3. present a review of the documented patterns of defoliating insect system behavior; and

4. review historical theories for the structure and behavior of these systems.

2.2 Methods Of Analysis

2.2.1 Analysis Of Equilibrium Structure

Natural populations are influenced by many factors. The proportional change in population size from one generation to the next is the simplest measure of the integrated effects of all factors. This proportional change is called "recruitment" (May 1977, Berryman 1978) and is a slightly different use of the term than in fisheries literature. Fisheries scientists generally take recruitment to mean the number of later adult animals produced from a given initial number of reproducing adults (Ricker 1954). The relationship between recruitment and parental population density or size can be graphically portrayed as a recruitment curve (Figure 1) and this curve represents how the integrated effects of all factors vary with population size. A recruitment of 1 at a particular population level means that there will, on average, be no change in population size from one generation to the next at that population level, provided all other factors also remain constant over time. A recruitment greater than 1 means an increasing population size, and a recruitment less than 1 means a decreasing popu-
Figure 1: Representative recruitment curves. Curve a contains a single stable equilibrium at f, while curve b contains a stable equilibrium at f' and an unstable equilibrium at u.
Consider curve a in Figure 1 and assume the following two conditions (I will relax these conditions later):

1. the magnitude of all factors affecting the population (e.g., habitat conditions, predator populations, climatic variables, etc.) remains constant; and

2. the effect of the rate of population change, the length of the time lags in any density-dependent population response, and the degree of non-linearity in the density-dependent response can be ignored.

The curve has but one point, f, at which recruitment, R, is 1. At any population size, N, greater than f, R < 1. This means that any population size which begins as a point above f will decrease toward f. At any N < f, R > 1. This means that any population size which begins at a level below f will increase toward f. All population sizes in this recruitment curve will move toward f and, therefore, f is a stable equilibrium (Southwood 1975).

Now consider curve b in Figure 1, and keep the magnitude of all factors affecting the population constant, save one. For discussion purposes, assume that this factor causes reduced mating success at low population levels. The same arguments for population levels near f' hold as for
point $f$ in curve $a$. However, at population level $u$, $R = 1$ as well but when $N < u$, $R < 1$ and the population level decreases toward 0. When $N > u$, $R > 1$ and the population level increases to $f'$. Population level $u$, then, is an unstable equilibrium (Southwood 1975).

But Figure 1 presents a static and unrealistic view of factors that affect population change. The position of the curve will change when the magnitude of any one process acting on the population changes. This is demonstrated in Figure 2, where the effect of a changing environment on a population is shown. For the sake of discussion, it is assumed that the effect is the same at any level of population; that is, the effect is density independent. As the environment becomes less favorable the unstable equilibrium moves to $u_1$ from $u_4$ (Figure 2a). The upper equilibrium shifts to $f_1$ from $f_4$. Given a sufficiently severe environment, only point $e$ will give a population recruitment of 1 or more. An even more severe environment will lower the recruitment curve even further, so that all recruitments are less than 1. The range of initial population sizes that ensure population persistence gradually narrows, while the range of initial population sizes that results in extinction gradually widens. A sufficiently severe environment will make any initial population level go to extinction. Changing processes acting on a population therefore change the equilibrium structure of that population by changing the number and position of population equilibria.
Figure 2: Effect of changing environmental conditions on population recruitment. Curves 1 to 5 in Figure a reflect the effects of an increasingly unfavorable environment. The curve in Figure b is an isorecruitment curve and contains all population equilibria for the range of environmental conditions.
A summary of the position of the equilibria as a function of the particular environmental factor of concern, shown in Figure 2b, will be termed an "isorecruitment curve" or "isocline" for the purposes of this thesis. The equilibrium structure of a population can be succinctly captured using isorecruitment curves.

2.2.2 Analysis Of Temporal Dynamics

The analysis above was conducted ignoring the rate and nature of population change and response. Equilibrium structure cannot by itself be used to indicate what the temporal dynamics of a population will be. Knowledge of the rate of population change, the length of time lags in any density-dependent response, and the degree of non-linearity in the density-dependent response are critically important as well (May 1976, May and Oster 1976). In general, population behavior will move from monotonic damping to damped oscillations to sustained stable cycles as the ratio of ratio of length of the time delay in the effect of the regulatory mechanism to the population return time increases for both differential and difference models. In difference models, a sufficiently large ratio will create chaotic behavior, largely indistinguishable from random process models (May and Oster 1976), although techniques for distinguishing deterministic behavior in apparently chaotic behavior have been developed (e.g., Schaffer and Kot in press). Shifts in behavior occur abruptly with smalll
changes in model parameters, and these shifts are called bifurcations. Bifurcations exist in the three models analyzed in Chapters 3 to 5, and these bifurcations represent the different classes of defoliating insect system behavior.

The points made above are especially relevant for the analyses of the difference models made in Chapters 3 to 5 of this thesis. Temporal behavior cannot easily be deduced from by analyzing equilibrium structure, and I will have to use model simulations to explain model behaviors.

2.3 The Equilibrium Structure Of Insect/Forest Systems

A central feature of most theories of defoliating insect system behavior is that of stability of numbers. Stable, low insect populations are a primary aim of biological control programs (Huffaker et al. 1971), and early population models were very much concerned with this concept. Thus, it is possible to speak of the "neutral stability" of the Lotka-Volterra model (Lotka 1926, Volterra 1928), the "global instability" of the Nicholson-Bailey model (Nicholson and Bailey 1935) and so on.

Voute (1947) first introduced the concept of "multiple stability", that insect species could have stable numbers at more than one level by proposing the notion of an "escape point" between endemic and epidemic population levels. Once a population had increased past this escape point, he argued, it would be very difficult to prevent it from reach-
ing epidemic levels.

Morris (1963) proposed that eastern spruce budworm had a stable equilibrium at a low population level and suggested that bird predation may be the mortality agent which creates this equilibrium. Takahashi (1964) applied Morris' concepts and suggested vertebrate predation could create a stable equilibrium at a low insect density. Clark (1964), working on Cardiaspina albitextura, and Readshaw (1965), working on sap-sucking insects, recognized 2 population "modes": one endemic and the other epidemic. Holling (1965) found that predators exhibiting a sigmoid functional response could potentially create a stable equilibrium in the prey population.

The concept of the occurrence and role of multiple equilibria was formalized by Holling (1973) who defined "stability domains" as regions of local stability separated by unstable equilibria. Southwood (1975, 1977) and Southwood and Comins (1976) developed an insect population model with 2 stable equilibria caused by the effects of predators and by intra-specific competition. They maintained that populations of K-selected animals living in relatively stable habitats should often be at the upper equilibrium set by intra-specific competition, while populations of r-selected animals living in ephemeral environments should shift from equilibrium to equilibrium. They described the dynamics of psyllids (Clark 1964) and European spruce sawfly (Neilson and Morris 1964) using their model.
The concept that multiple equilibria exist in insect populations has been developed on largely theoretical grounds (Holling 1973, May 1977, Berryman 1978, May 1979). Empirical evidence is based largely on observations of predation effects on endemic insect population densities (e.g., Holling 1956, Mason and Torgerson 1977, Campbell and Sloan 1978, Rose and Harmsen 1978). But, the concept is not unanimously accepted and various workers argue for alternate explanations for the same observations (e.g., Royama 1984). Critical field experiments which would test the multiple stability concept have not been undertaken. I will come back to this point in the invalidation and summary chapters of the thesis.

2.4 Hypotheses For Insect/Forest System Behavior

This section reviews existing theories for defoliating insect system behavior. I will return to the ideas presented here and in Chapter 3 to examine how this thesis compares with historical attempts to understand and explain the behavior of these systems. Throughout the following discussion, I will make extensive use of isorecruitment curves to present the theories in a consistent framework that allows for easy comparison among them. I will assume, in using these curves, that parameter conditions give rise to damped oscillations. The techniques of Rosenzweig and MacArthur (1963) will be used in the analysis.

2.4.1 Predation And Parasitism
Predation and parasitism have been cited as important regulating factors of insect populations (Miller 1966, Baltensweiler 1968, Bigger 1973, Holmes et al. 1979, Hanski and Otronon 1985, Smith 1985). The first population models (Lotka 1926, Voltera 1928) suggested that predators and parasitoids could theoretically regulate insect numbers. Nicholson and Bailey (1935) developed a population model in which the predator could drive the prey to extinction and so itself become extinct. Hairston et al. (1961) argued for the role of predation because of the general absence of food depletion by herbivores.

It has been shown that the functional response of a predator can be one of 4 types (Holling and Buckingham 1976) each of which confers different equilibrium structures to the prey, given no predator numerical response. The total predator or parasite response (functional plus numerical) has very different implications for predator dynamics. Three examples (Figure 3) reflect different situations which will be encountered in the analysis of the three simulation models in later chapters.

The first (Figure 3a) is for a prey population with a single stable surface. This situation creates a predator isocline which is always to the right of the peak of the prey isocline and therefore temporal behavior characterized by dampening oscillations. The second (Figure 3b) is for a prey population which has depensatory mortality caused, say, by a Type II functional response. In this situation, the
Figure 3: Alternate configurations of predatory-prey iso-recruitment curves. Each creates different stability properties of the system. a - prey has a single stable surface. This means that predator and prey populations oscillate around the joint equilibrium. b - the prey has a stable surface at high densities and an unstable surface at lower densities. The prey, followed by the predator, can go extinct if the joint equilibrium remains on the unstable surface. c - the prey has two stable surfaces separated by an unstable surface.
potential exists for the predatory isocline to be to the left of the peak of the prey isocline. This situation causes increasing oscillations resulting in eventual extinction of both the prey and the predator.

The third (Figure 3c) is for a prey population which has a population isocline with two stable surfaces separated by an unstable surface. This can be caused by, say, a prey-switching predator exhibiting a Type III functional response. The system persists in this case even though the common equilibrium may be to the left of the peak of the prey isocline. The switching predator creates a prey "refuge" at low prey densities which prevent prey, and therefore, predator, extinction.

2.4.2 Nutrient Limitation And Foliage Quality

The nutritional quality of plant parts favored by insects for feeding has been cited as a mechanism evolved by the plant for controlling numbers of its insect enemies (Wallner and Walton 1979, Haukioja 1980, Rhoades 1983, 1985). White (1969, 1974, 1976, 1978) maintains that the food resource for insects is usually nitrogen deficient and therefore nutritionally inadequate for proper herbivore survival and fecundity. White hypothesizes that, when the host plant is stressed through lack of water, it produces relatively nitrogen-rich foliage; consumption of higher quality food gives better survival of the very young insects, usually the first instars which initiate feeding. This, in
turn, leads to higher fecundity and increase in numbers. The passing of drought conditions leads the plant to be able to produce nitrogen poor food which once again creates poor survival for early instars and lowered fecundity. Haukioja and Hakala (1975) and Rhoades (1985) hypothesize that plants, rather than regulating necessary chemicals for insect growth, regulate chemicals in their tissues which are detrimental to insect populations. Rhodes distinguishes two types of compounds in the host plant: "qualitative" compounds -- compounds of limited use a defensive agents but energetically cheap to manufacture -- and "quantitative" compounds -- effective defensive compounds which are energetically expensive to make -- and argues that changes in the relative production of each, caused by environmental stress on the plant, determine insect survival and therefore population change.

The effects of changing food quality on the equilibrium structure of an insect population can be pictured as a change in foliage abundance and quality (Figure 4). In this case, the foliage is the prey and the defoliator becomes the predator. Usually the foliage quality is too poor for good survival and fecundity and can only support a low population (Figure 4, curve a). The common equilibrium is at a high foliage biomass and low defoliator density. When the host plant is stressed by some event or process and is forced to produce better quality food, the resource base can support a higher defoliator density. The predator isocline shifts to
Figure 4: Isorecruitment curve representation of foliage quality hypotheses. The predator (i.e., defoliator) curve shifts from a to b (endemic to epidemic) as foliage quality improves because a given amount of good quality foliage is able to support a greater number of defoliators than the same amount of poor quality foliage. Populations cycle around the equilibria.
the left in Figure 4, to curve b. This causes the common equilibrium to move to a condition of high defoliator density and decreased foliage biomass. Removal of the stress on the plant re-creates the conditions for curve a and the population collapses. McNeill and Lawton (1979) provide a general review of the roles of predation, parasitism, nutrient availability, and chemical defense on insect populations.

A drawback of the nutrient/chemical regulation hypotheses is that the insect is regarded as a non-evolving actor in the dynamics of defoliating insect systems. Changing susceptibilities of insect species to plant compounds are not considered. The specific theories described above can therefore not explain phenomena such as different outbreak frequencies for defoliators with similar life histories feeding on the same resource (e.g., eastern black-headed budworm and eastern spruce budworm (McNamee 1977)).

Also, recall that the key life history stage in the food quality theories described above is the stage in which feeding is initiated. Changes in nutrient quality affect survival of this stage which then affects population levels. If this hypothesis is valid, measures of population change such as population recruitment and fecundity should be positively correlated with the survival rate of larvae which initiate feeding. Unfortunately, very few research programs have estimated early larval survival rates, probably because those stages cause so little of the total defoliation.
However, the proper types of data for testing the food quality hypothesis have been collected for the pine looper (Klomp 1966), European pine sawfly (Lyons et al. 1972), and jack pine sawfly (McLeod 1977a).

Correlations between survival of the first larval feeding stage and fecundity, then population recruitment (Table I) are inconclusive. 3 out of 6 correlations are significant at the level of .05. This is a crude test but it does indicate that existing data do not support the nutrient quality hypothesis.

2.4.3 Qualitative Differences Between Individuals

Differences between individuals of a population may be important in causing temporal change in the density of that population. The hypothesis, first proposed by Chitty (1960), is that species are capable of regulating their population levels with genetically and intrinsically induced changes in the viability of individuals in the population. Wellington (1957, 1960, 1964), working on western tent caterpillar, modified Chitty's theory for western tent caterpillar to be primarily physiological, rather than genetically based.

Wellington found western tent caterpillar individuals could be classified into essentially two types: active and sluggish. Active individuals have a high feeding rate, are good dispersers and can survive well under poor environmental conditions. Sluggish individuals are the opposite.
Table I: Correlations of fecundity and population recruitment to early instar larval survival for three forest pests.

<table>
<thead>
<tr>
<th>INSECT SPECIES</th>
<th>DATA SOURCE</th>
<th>FECUNDITY VERSUS EARLY LARVAL SURVIVAL</th>
<th>RECRUITMENT VERSUS EARLY LARVAL SURVIVAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jack pine</td>
<td>McLeod (1977a)</td>
<td>3</td>
<td>.148</td>
</tr>
<tr>
<td>Sawfly</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pine Looper</td>
<td>Klomp (1966)</td>
<td>9</td>
<td>.002</td>
</tr>
<tr>
<td>European Pine</td>
<td>Lyons et al. (1972)</td>
<td>8</td>
<td>.012</td>
</tr>
<tr>
<td>Sawfly</td>
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Populations just beginning to increase are composed largely of active individuals which can emigrate and colonize other sites and have high recruitment (Figure 5). Western tent caterpillar populations increase until the food resource becomes limiting. The partitioning of maternal food reserves is unequal so that some of the eggs laid in a population which is food-limited contain less than optimal food reserves. These hatch to become sluggish individuals. The feedback is perpetuated, with the sluggish individuals having lower and lower food consumption and producing a higher and higher proportion of sluggish individuals in the succeeding generations. The deterioration in health of the population is exacerbated by a high incidence of disease which develops in sluggish individuals and spreads to both sluggish and active individuals. Local populations eventually decline to extinction.

The persistence of the species over large areas is ensured by the fact that not all sites are in the same point in the population cycle. This means that active individuals always exist to colonize locations which have gone extinct. A similar hypothesis was proposed for explaining the dynamics of the larch budmoth/Alpine larch system (Baltensweiler 1964).

2.4.4 Genetic Feedback

Pimentel (1961) and Pimentel and Stone (1968) proposed a genetic feedback mechanism to explain fluctuations in
Figure 5: Isorecruitment curve representation of the hypothesis of individual differences. The increasing proportion of sluggish individuals in the defoliator population shifts the predator curve shifts to the right, eventually past foliage curve. This causes a collapse of the defoliator population. Dispersal serves to recolonize sites where the defoliator has gone extinct.
insect density. This mechanism operates as a negative feedback between parasitoid-host and/or herbivore plant levels through the effects of density on intensity of selection for less tightly coupled (i.e., less efficient predation) interactions. This type of mechanism is thought to be most important when a species is introduced to a new environment; initial violent fluctuations in populations of the species at both trophic levels decrease over time as genetic feedback acts to weaken the interaction between the species (Figure 6).

2.4.5 Dispersal

The processes of dispersal have been shown to be important in the population dynamics of many forest defoliators (Greenbank 1957, Leonard 1970a, 1970b, Clark 1979). Huffaker (1958) using laboratory experiments, and Gilpin (1975) and Hilborn (1976, 1978), using simulation models, have shown that spatial heterogeneity and dispersal can stabilize, or at least allow persistence of, predator and prey populations that are unstable in local, spatially homogeneous areas. The theory of individual differences proposed by Wellington (1957, 1960, 1964) requires dispersal between sites as a mechanism for redistributing active, vigorous insects. Ormond (1977) suggests that insects whose habitat distribution is patchy may have evolved the capacity to produce outbreaks to provide a source of insects for redistribution and therefore avoid the consequences of local extinction by predators.
Figure 6: Iso-recruitment curve representation of the genetic feedback hypotheses. The strength of the negative feedback between predator and prey populations changes via changes in selection pressure through time. This causes dampening oscillations to a joint stable equilibrium from the time of introduction.
Sufficient immigration to a site can swamp any equilibrium structure created by local processes such as predation (Figure 7). The effect of a given level of immigration will be more pronounced at lower population sizes than at high because the effect is proportionately much greater at lower population levels. The effect of emigration on local equilibrium structure is more complicated and depends very much on the characteristics of the exodus response (Clark 1979).

2.4.5 Density Independent Mechanisms

Weather and climate have long been thought to determine the pattern of insect numbers (Larsson and Tenow 1984, Thomsen et al. 1984). The classic examples were given by Andrewartha and Birch (1954) who argued that insect abundance was limited by the length of time conditions for feeding and reproduction were favorable; climatic factors were cited as primary agents affecting the length of time available for these processes. White (1969, 1974, 1976, 1978) maintained that the available nitrogen in the food supply, which determines the vigor of the population, is determined largely by climatic conditions. Outbreaks of many forest defoliators are sometimes preceded by a few generations of weather favorable to the insect (Greenbank 1956, Stark 1959, Lessard 1974) and collapse of infestations often coincides with unfavorable weather conditions (Silver 1960, 1963, Campbell 1979). The effect of density independent processes on the equilibrium structure of a population is simple (Fig-
Figure 7: Isorecruitment curve representation of the effects of immigration. The effect of constant immigration is most pronounced at low densities. Immigration transforms an unstable joint equilibrium between predator and prey (prey curve a) to a stable joint equilibrium (prey curve b).
Density independent mechanisms act equally at all population levels and therefore shift the isorecruitment curve equally at all population levels. These mechanisms cannot be involved in "control", "regulation", or "limitation" in so far as these concepts are defined in terms of feedback mechanisms that act differently at different population sizes.

2.4.6 Existing Integrative Theories

The above sections describe the consequences for numerical behavior of populations arising from the effects of single processes. But, a number of integrative theories exist for explaining the dynamics of particular defoliating insect systems. For example, the studies of Wellington (1957, 1960, 1964) and Wellington et al. (1975) for western tent caterpillar and of Baltensweiler (1964) and Baltensweiler et al. (1977), for example, integrate the dynamics of natural enemy complexes, particularly disease epizootics, effects of individual differences in a population, and dispersal among sites to explain the behavior of these systems.

There are also integrative theories which attempt to explain the behavior of many defoliating insect systems. For example, the synoptic model of Southwood and Comins (1977) uses predation (creating a potential endemic stable equilibrium), intra-specific competition and habitat stability to explain the dynamics of five insect pest systems.
Figure 8: Isorecruitment curve representation of the effects of density independent processes. Density independent processes acting on the prey shift the prey curve equally at all population levels and therefore do not change the equilibrium structure of the system.
There are two integrative theories for the behavior of the eastern spruce budworm system. Clark and Holling (1979) and Clark (1979), using detailed analyses of the Green River, New Brunswick data (Morris 1963), integrate effects of intra-specific competition, vertebrate predation, dispersal and dispersal effects on survival, weather effects on survival, and foliage and forest dynamics in their theory for the behavior of the eastern spruce budworm system. They maintain that the budworm system is multiply stable: a low density stability region caused largely by avian predation on large larvae, and a high density stability region caused by foliage limitation. They also maintain that outbreaks are initiated and terminated through the increased dispersal survival of first and second instar larvae, which is related to forest maturity and branch surface area (Clark 1979). On the other hand, Royama (1984), in his analysis of the Green River data, hypothesizes that there is no low density stability region, largely because the population densities appear to be more cyclical than bimodal (Royama 1984, Figure 1). He also hypothesizes that outbreak initiation and termination is caused by changes in large larval survival which occurs through changes in parasitism, microsporidia, and viral disease levels. Also, although I have bounded spatial dynamics of defoliating insect systems out of this thesis, it is worth mentioning that these workers agree that adult dispersal among areas is less critical to explaining budworm population dynamics than are local, or site, processes.
Essentially, the difference in hypothesized explanations for local dynamics of the eastern spruce budworm system, developed with two models utilizing essentially the same dataset, clearly demonstrates the need to use models to develop field testable theories, and to conduct the field tests in an attempt to invalidate the theory (see Chapter 7). The lack of a bimodal distribution of budworm population densities does not mean that a lower stability region caused by bird predation does not exist. A lower stability region (and therefore equilibrium) may exist, but its position very likely shifts in response to changes in other attributes of the system such as forest growth. The key question related to the issue of whether the budworm population is or is not multiply stable is not whether the historical data indicate lower stability regions, but rather would the behavior of the budworm population be any different if bird predation did not exist. This is not known, and I outline what the necessary field experiment would be to test this in Chapter 7. Similarly, the differences in hypothesized causes of outbreak initiation and termination (large larval survival versus small larval survival) can only be conclusively tested with the proper field manipulations.

2.5 Patterns Of Insect/Forest System Behavior

It is important to compare the behaviors predicted by the integrative theory I will develop with real behaviors of defoliating insect systems, both in terms of temporal pat-
terns and of the processes which give rise to the behavior. I conducted a literature and data review for as many defoliating insect systems as possible to provide the basis for comparison. I reviewed 22 defoliating insect systems and gathered information for 38 different behaviors exhibited by these systems. These systems, taken together, represent examples from a wide range of geographical location, type of forest and tree species affected, degree of economic importance, and level of understanding of factors important in system behavior.

2.5.1 Sources of Information and Structure of the Review

I used three sources of information for this review: the general forest entomological literature; detailed scientific reviews summarizing results of long term studies; and long term insect population density data collected either as a part of pest surveys or during long term research investigations. Long term population density data existed for twelve defoliating insect systems. The data for these systems are summarized in Appendix I, while their data sources are described in Table II.

The following information, if it was available, was gathered in order to describe the qualitative behavior of each system:

1. the primary host tree species;

2. the time period of interest. As described in
Table II: Sources of insect population data.
BCFIDS - British Columbia Forest Insect and Disease Survey; CFS - Canadian Forest Service; USFS - U.S. Forest Service

<table>
<thead>
<tr>
<th>SPECIES</th>
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<td>Gypsy Moth</td>
<td>egg mass surveys, USFS</td>
<td>Campbell and Sloan (1978)</td>
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</table>
Chapter 1, many defoliating insect systems have exhibited different behaviors during different time intervals;

3. the geographical location of interest. As described in Chapter 1, many defoliating insect systems exhibit different behaviors in different parts of its range;

4. the length of time between outbreaks;

5. the duration of outbreaks;

6. factors which have been inferred in the decline of outbreaks;

7. any other factors which have been implicated in determining the dynamics of the system; and

8. the effect of outbreaks on the host forest.

The duration of outbreaks was determined from reports in the literature and from the results of spectral analyses done on the datasets for twelve defoliating insect systems (Jenkins and Watt 1968, summarized in Appendix I). The MIDAS statistical package was used to conduct these spectral analyses (Fox and Guire 1976).

2.5.2 Results

There are four different categories of outbreak periodicities represented in these systems (Table III):
Table III: Patterns of insect/forest system behavior. References for information provided are listed in Table IV. * - for all documented behavior; ---- - no outbreaks; †††† - continual outbreaks; A - no mortality; B - mortality primarily in suppressed trees; C - mortality in suppressed trees and some healthy trees; D - mortality in healthy and suppressed trees; ?? - information not known; blank - information provided elsewhere in table or not necessary. Second set of numbers under outbreak period refers to periodicity calculated by spectral analysis (Appendix I).

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<td>Carroll (1954), Canada (1939 to present)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eastern Blackheaded Budworm</td>
<td>Miller (1966), Miller and Marshall (1970), Canada (1939 to present)</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Eastern Spruce Budworm</td>
<td>Morris (1963), Blais (1968, 1974), Miller (1975), Clark (1979), Clark and Holling (1979), Morris (1958), Wotton and Jones (1975), Canada (1939 to present)</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>European Pine Sawfly</td>
<td>Lyons et al. (1972)</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>European Spruce Sawfly</td>
<td>Neilson and Morris (1964), Balch and Bird (1944)</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Green-striped Forest Looper</td>
<td>Dawson (1970), Evans (1962)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Gypsy Moth</td>
<td>Bess (1961), Campbell and Sloan (1978), Campbell et al. (1977), Kaya (1976), Maksimovic (1953), Simionescu (1973)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jack Pine Budworm</td>
<td>Canada (1939 to present)</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table IV: continued

<table>
<thead>
<tr>
<th>INSECT</th>
<th>LITERATURE USED</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larch Budmoth</td>
<td>Baltensweiler (1968), Baltensweiler et al. (1977), Fischlin and Baltensweiler (1977)</td>
</tr>
<tr>
<td>Larch Sawfly</td>
<td>Canada (1939 to present), Turnock (1972), Graham (1952), Coppel and Leius (1955)</td>
</tr>
<tr>
<td>Pine Looper</td>
<td>Klomp (1966), Varley (1949)</td>
</tr>
<tr>
<td>Saddlebacked Looper</td>
<td>Silver (1961), Canada (1939 to present)</td>
</tr>
<tr>
<td>Spruce Budmoth</td>
<td>Carrow (1985)</td>
</tr>
<tr>
<td>Western Blackheaded Budworm</td>
<td>Canada (1939 to present), McCambridge and Downing (1960)</td>
</tr>
<tr>
<td>Western False Hemlock Looper</td>
<td>Klein and Minnoch (1969), Canada (1939 to present)</td>
</tr>
<tr>
<td>Western Hemlock Looper</td>
<td>Furniss and Carolin (1977), Canada (1939 to present)</td>
</tr>
<tr>
<td>Western Spruce Budworm</td>
<td>Johnson and Denton (1975), Canada (1939 to present), Torgerson and Campbell (1982), Campbell and Torgerson (1983), Campbell et al. (1983)</td>
</tr>
<tr>
<td>Western Tent Caterpillar</td>
<td>Canada (1939 to present), Wellington (1957, 1960, 1964)</td>
</tr>
<tr>
<td>Winter Moth</td>
<td>Embree (1965), Cuming (1961), Canada (1939 to present), Varley and Gradwell (1965), Hassell (1976)</td>
</tr>
</tbody>
</table>
1. a lack of outbreaks;

2. a continual outbreak;

3. sporadic outbreaks; and

4. outbreaks ranging in periodicity from 2 years to about 90 years.

The preponderance of outbreak periodicities appear to be at 6-12 years (or 6-12 defoliator generations in the case of divoltine defoliators). Viral disease or parasitism are factors most often implicated in the decline of outbreaks, although starvation of defoliators is mentioned often as a causal mechanism for outbreak decline. Other factors, such as foliage quality and individual differences are cited, although much less often than the above factors.

Host forests generally suffer either little or no mortality from outbreaks or very heavy mortality. Furthermore, the type of host damage incurred does not seem to depend on the outbreak periodicity. Forests in systems which have experienced continual outbreaks can experience little mortality (e.g., gypsy moth) while forests in systems which experience sporadic outbreaks can suffer very heavy mortality (e.g., eastern hemlock looper, Douglas-fir tussock moth). Also, jack pine can suffer very heavy mortality when defoliated by jack pine sawfly, but only moderate mortality when defoliated by jack pine budworm.
Predation, particularly vertebrate predation by birds and small mammals, is cited very often as a factor which influences defoliator populations. In most systems in which it is understood, vertebrate predation has the greatest effect on the defoliator at low population levels.

The picture from this review, therefore, is one of a small number of different classes of defoliator population behavior, albeit with a wide variety of outbreak periodicities. Also, it appears that only a small set of variables and processes have been implicated in the dynamics of defoliator populations: a defoliator whose dynamics is influenced by starvation, vertebrate predation, parasitism, and viral diseases. The factors which influence the dynamics of the forest are less certain.
3.0 THE EASTERN BLACKHEADED BUDWORM SYSTEM

3.1 Introduction

Chapter 2 described the methods of analysis which will be used in this thesis, provided an overview of some of the important historical theories for the behavior of insect/forest systems, and described the types of behavior exhibited by insect/forest systems. This and the following two chapters develop evidence which will be used to develop the integrative theory for the behavior of insect/forest systems. This evidence is in the form of detailed analyses of three defoliating insect systems and models: the eastern blackheaded budworm; the eastern spruce budworm; and the jack pine sawfly.

3.2 The Eastern Blackheaded Budworm System

Eastern blackheaded budworm is a native defoliating insect of the eastern North American coniferous forest. Its favored host tree is balsam fir, *Abies balsamea*; it will also feed on white spruce, *Picea glauca*, in later instars but it does not survive well on other tree species (Miller 1966).

The budworm is found from northern Manitoba south and east to Newfoundland (McCambridge and Downing 1960). Intensive population studies commenced on blackheaded budworm as an offshoot to the Green River eastern spruce budworm project in New Brunswick in the 1950s and 1960s. No management activities have been directed at this defoliator, although
populations of the insect have undoubtedly been affected by the application of insecticides for control of eastern spruce budworm in New Brunswick.

3.2.1 Documented Behavior

The system has exhibited essentially two different types of behavior (Canada 1939 to 1982, Miller 1966, Table III). First, outbreaks have been observed regularly in the Maritimes since the early 1900s. All recorded outbreaks have followed a similar pattern. Populations increase to outbreak levels every 12 to 16 years and persist at these high levels for 2 to 4 years. These outbreaks cause heavy defoliation and consequent growth reduction of mature host trees. However, they cause very little mortality of mature overstory timber. Parasitism rates are usually low in all parts of the insect population cycle except in the declining years of outbreaks, when rates may reach 80% to 97% (Miller 1966).

A second type of behavior occurs over much of the geographical range of the insect. In these areas the insect is regularly recovered in Forest Insect Survey samples, but persistently remains at endemic levels. Naturally, in these areas, defoliation is low and there is no tree damage.
3.3 System Description

3.3.1 The Defoliator

The life history of eastern blackheaded budworm has been described by several authors (Morris 1958, McCambridge and Downing 1960, Miller 1966). The insect is univoltine. Eggs are laid in the early fall and the budworm passes the winter as a diapausing egg. First instar larval emergence occurs in late May the following year. There are five feeding larval instars and pupation occurs in late July in the sites where the fifth instar larvae last fed. The insect prefers the current year's foliage but will feed on older foliage if necessary. Some larval drop and dispersal has been observed (Miller 1966) but it does not appear to be an obligatory process for the species. Adult moth dispersal has also been occasionally observed (Miller 1966) but its importance in the spatial dynamics of the population are not known.

3.3.2 Natural Enemies

A large complex of parasitoid species has been recovered from eastern blackheaded budworm (Miller 1966). Parasitism rates have been recorded to vary from 3% in the early stages of an outbreak to 97% in the decline phase of infestations. A species of *Ascogaster* appears to be the most important species, as it is the most common species recovered during outbreak declines.

Bird predation has been extensively studied (Gage et
Avian predation occurs on all life stages of the budworm, but is concentrated on the large fifth instar and pupal stages. Avian predation rates are much higher at low budworm densities than at high (Miller and Mook 1970).

3.3.3 The Forest and Foliage

Balsam fir is the dominant tree species of the boreal forest of eastern North America and is a co-dominant species, along with white, red, and black spruce, of the eastern North American coniferous forest (Bakuzis et al. 1965). Balsam fir is a shade tolerant species (Bakuzis et al. 1965), and appears to exist on a "pathological rotation" of 70 to 100 years (Marchand 1984) and decline of balsam fir from biotic or abiotic events occurs in mature stands from eastern spruce budworm (Blais 1968), wind (Sprugel 1976) or root diseases and rots (Blum et al. 1983). Removal of the overstory in pathological rotation dramatically increases growth of previously suppressed balsam fir (Blais 1952).

Balsam fir and white spruce retain approximately eight year classes of foliage. The complement of new foliage flushes in late April or early May, very near the time eastern blackheaded budworm emerge from diapause. White spruce foliage flushes approximately 2 weeks later than balsam fir (Miller 1963).

3.4 Model Description

An initial simulation model of the dynamics of the
system was constructed as part of a baccalaureate thesis (McNamee 1977, pp. 80-100). The model was subsequently revised and elaborated; a summary of the final model is given in McNamee (1979).

3.4.1 Spatial And Temporal Characteristics

The model mimics system behavior in a uniform stand of balsam fir large enough that population losses or gains due to insect movement into and out of the stand are negligible. Budworm habitat within the stand is described in square meters of branch surface area. Forest and foliage dynamics are simulated annually but most of the interactions between budworm and its environment occur on specific instars during the model year.

3.4.2 Forest Dynamics

The model uses the forest and foliage submodels developed by Jones (1977a) for the eastern spruce budworm simulation model. The rationale for this is that both defoliators occupy the same forest habitat, prefer the same host tree species and age classes of foliage, and feed on the host species at similar time of the year (McNamee 1977). Responses of the foliage and the forest to the same levels of defoliation by both forest insects is therefore likely to be similar, assuming there are no differences in tree response for a given level of defoliation by either budworm.

The forest is represented as 75 age classes of host trees. Each tree age class is characterized by three relevant
attributes: the proportion of the land area it occupies (Jones 1977a, p.101); the branch surface area per acre of forest if each acre were entirely in trees of that age class (Jones 1977a, p. 103); and susceptibility of the age class to mortality from budworm defoliation (Jones 1977a, p. 113). Trees less than 22 years of age are assumed to be immune to budworm attack. The ratio of existing branch surface area to the branch surface area of a 40 year old stand is used as a measure of the degree of forest maturity.

Forest growth is simulated by annually aging the age class parcels of land after accounting for natural and budworm-induced mortality. Aging involves changes in branch area, while area occupied by an age class changes only due to mortality. All mortality is placed into the youngest age class, implying immediate regeneration.

The fraction of trees killed by budworm in each age class is a function of the age-specific forest susceptibility from budworm mortality (Jones 1977a, p.113) and the defoliation stress caused by budworm defoliation (Jones 1977a, p.112). Older forest age classes have a higher susceptibility to mortality to budworm defoliation, while younger age classes are completely immune to defoliation and therefore to this mortality. Also, defoliation stress does not begin to occur until old foliage biomass begins to decline.

3.4.3 Foliage Dynamics
Although balsam fir and white spruce retain approximately 8 year classes of foliage (Bakuzis et al. 1965), the model considers only dynamics of two classes: current year's foliage; and an aggregated class of old foliage (1+ years old). Foliage is measured in relative units, as proportion of maximum possible new foliage biomass per m of branch.

Non-susceptible age classes are assumed to always have a full complement of foliage. New foliage biomass for susceptible forest age classes produced at the start of each year is proportional to the total foliage biomass left at the end of the previous year (Jones 1977a, p.107). Old foliage biomass is updated using density-dependent survival functions for remaining old and new foliage (Jones 1977a, p.107). Old foliage dynamics are structured so that a tree will retain a higher proportion of its new foliage as defoliation increases. The forest, in effect, compensates for defoliation by retaining a higher proportion of remaining foliage from the current year. New foliage levels in budworm susceptible age classes are modified to account for the recruitment of newly susceptible age classes, using a branch surface area-weighted average of foliage biomass in the susceptible and newly susceptible age classes.

3.4.4 Insect Dynamics

Base Population Parameters

Miller (1966) presents a survivorship curve for eastern blackheaded budworm and documents unpublished findings of
other workers on budworm mortality rates. The adult, egg, early larval, and pupal stages are characterized by relatively low and constant mortality rates. The large larval stage is characterized by highly variable mortality rates. Miller (1966) attributes the changes in large larval mortality to avian predation and parasitism.

It is impossible to disaggregate the published large larval survival rates into "predator and parasitoid induced" and "natural". The published rates, however, were taken from studies done in mature forest stands in an inter-outbreak period. Parasitism rates are likely to have been low (Miller 1966) and avian predation levels are also likely lower than in younger stands (Section 3.4.5). I therefore adopted the rates from Miller (1966) as baseline survival rates (Table V).

The sex ratio of adults is relatively constant in non-outbreak situations (Miller 1966). Although evidence from other insect/forest systems indicate the sex ratio would likely change under conditions of low foliage because female larvae must consume greater amounts of foliage for egg development (Brookes et al 1979, Doane and McManus 1981, Morris 1963), I assumed it remains constant, irrespective of the condition of the budworm (Table V).

Miller (1966) published a number of fecundity estimates for the budworm in non-outbreak situations in a series of stands. The mean of these fecundities is used as the max-
Table V: Baseline population parameters for eastern blackheaded budworm. Parameters derived from Miller (1966).

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Egg Survival Rate</td>
<td>0.85</td>
</tr>
<tr>
<td>2. Small Larval Survival Rate</td>
<td>0.60</td>
</tr>
<tr>
<td>3. Large Larval Survival Rate</td>
<td>0.25</td>
</tr>
<tr>
<td>4. Pupal Survival Rate</td>
<td>0.71</td>
</tr>
<tr>
<td>5. Adult Survival Rate</td>
<td>1.0</td>
</tr>
<tr>
<td>6. Adult Sex Ratio</td>
<td>0.53</td>
</tr>
<tr>
<td>7. Maximum Fecundity</td>
<td>88</td>
</tr>
<tr>
<td>8. Baseline Generation Survival</td>
<td>0.048</td>
</tr>
<tr>
<td>(product of 1 through 6)</td>
<td></td>
</tr>
<tr>
<td>(product of 1 through 7)</td>
<td></td>
</tr>
</tbody>
</table>
imum fecundity in the model (Table V). This assumes that nutritional conditions for budworm will be most favorable at low population levels.

Weather effects on budworm are simulated by randomly varying the large larval survival between 0.76 and 1.29 as is done in the eastern spruce budworm model (Jones 1977a, p. 121).

The baseline generation survival is 0.048 and the maximum recruitment, the product of the generation survival and maximum fecundity, is 4.22, given the survival rates, sex ratio, and maximum fecundity (Table V). This means that, in the absence of any other factors, budworm populations in the model will increase approximately 4-fold per year.

**Feeding And Feeding Effects**

Eastern blackheaded budworm meets most of its foliage requirements for maturation in the last larval stage. Miller (1966) reports lowered larval survival and fecundity at high population levels. Intra-specific competition is hypothesized to be the cause of these two phenomena.

The feeding submodel is a predator-prey model. It is assumed that an individual larva has a functional response to its "prey", the foliage. This response is shaped by the requirements of the larva for maintenance, growth, and reproduction. Competition among larvae for foliage modifies this response.
The instantaneous functional response is:

\[ q = m, \quad \text{where} \]

- \( q \) is the per larva consumption of foliage; and
- \( m \) is the number of foliage units (Section 3.4.3) required by a larva for survival and maximum growth and reproduction.

Equation 1 implies that food requirements are constant over all foliage densities.

The total food requirement \((A)\) of the whole population \((N)\) is therefore:

\[ A = (q) (N), \quad \text{where} \]

No estimates of \( q \) are available from previous work on black-headed budworm. I elected to use an estimate modified from the eastern spruce budworm model.

Eastern spruce budworm is assumed to require \( .0074 \) foliage units. \( q \) for blackheaded budworm was estimated as:

\[ q = \frac{.0074HCW_{\text{bhb}}}{HCW_{\text{esb}}}, \quad \text{where} \]

- \( HCW \) is the last instar head capsule width for each species.

\( HCW \) is \( 1.36 \text{ mm} \) (Miller 1966) and \( HCW \) is \( 1.44 \text{ mm} \) (Morris 1963); \( q \) is set to \( .007 \). Equation 3 assumes a linear relationship between food requirements and head capsule width,
even though the relationship is likely to be allometric. This is a reasonable assumption, since the differences in head capsule width between the species is less than 6%.

A random competition model, analogous to that developed by Thompson (1924) for parasitoids, is used to compute realized intake of foliage:

\[ E = F \left(1 - e^{-A/F}\right), \]

where

\[ E \] is the units of foliage consumed by all larvae; and

\[ F \] is the foliage density.

Equation 4 is applied twice, first for feeding on new foliage and second for feeding on old foliage which occurs if food requirements have not been met by consumption of new foliage.

The budworm population's food requirements for old foliage \( (A') \) are:

\[ A' = A - E \]

and old foliage \( (F') \) consumption \( (E') \) is calculated as:

\[ E' = F' \left(1 - e^{-A'/F'}\right) \]

There are no data in the literature on the exact relationship between the quantity of foliage consumed and
survival and fecundity for eastern blackheaded budworm. I assumed both relationships to be simple linear ones. Therefore, large larval survival is modified for starvation effects by:

\[
s = \frac{(E + 0.8E')}{(qN)}, \quad (7)
\]

where

- \(s\) is a survival rate applied to large larvae,
- \(E\) is a proportion to account for the assumed lower quality of older foliage to budworm.

Actual fecundity, \(b\), is calculated by:

\[
b = sB, \quad (8)
\]

where

- \(B\) is the maximum possible fecundity (Table V).

3.4.5 Natural Enemy Dynamics

Parasitism

The majority of parasitoid species which respond numerically to changing blackheaded budworm densities attack the young larvae and emerge from the large larvae (Miller 1966). Of these, a species of *Ascogaster* appears to be the most important. I modelled the dynamics of this species and assumed it to be representative of the guild of parasitoids that attack small larvae and emerge from large ones.
Unfortunately, I could find no data on the bionomics of the species. Cox (1928) presents a detailed analysis of the biology and behavior of a conspecific, *Ascogaster carpopus*. The biology and behavior of this parasitoid was used as a surrogate for the species that attacks budworm.

The model of parasitoid dynamics is very simple. The number of adult female parasitoids attacking early budworm larvae in year $t$ ($P^*_t$) is given by:

$$P^*_t = S_p S_h N_{t-1} \left\{ 1 - \frac{aT N_{t-1}^t P_{t-1}^{t-1}}{1 + a h N_t^{t-1}} \right\}$$

where:

- $N_{t-1}$ is the number of host larvae in year $t-1$;
- $S_h$ is the survival rate of budworm from the time of parasitoid attack to parasitoid progeny emergence; and
- $S_p$ is the survival rate of parasitoids from emergence to attack (includes sex ratio);
- $a$ is the rate of successful search by the parasitoid for budworm;
- $T$ is the total time the parasitoid searches for budworm;
- $h$ is the handling time, or the time taken by the parasitoid from the beginning of attack to the resumption of search; and
k is the dispersion coefficient of the negative binomial distribution.

Equation 9 is an instantaneous functional response, a competition submodel to account for super-parasitism effects (Griffiths and Holling 1969, Mace et al. 1978), and a series of survival functions which compute the number of attacking parasitoids from the number of parasitized budworm in the previous generation. S is calculated in the defoliator submodel from natural and starvation mortality. Budworm feeding rates and susceptibility to other forms of predation are assumed to be the same for parasitized and non-parasitized hosts.

The Functional Response

I used the Type 2 functional response form representative of a predator searching for a single prey type (Holling 1959, but see Hassell et al. 1977) because Ascogaster is capable of causing heavy mortality to its host (Miller 1966) and is therefore likely to be monophagous and an obligatory parasitoid of the budworm (Price 1975).

Holling (1965) and McLeod (1976) show that the functional response parameters can be estimated from simple biological knowledge about the behavior of the predator and prey. Ascogaster females are long-lived with a mean life span of 36 days. The adults search only by day; I set T to 288 hours, assuming 8 hours per day is spent searching (J.M. McLeod, pers. comm.). The parasitoid fecundity is 360 eggs
(Cox 1928). This means that \( h \), the handling time, is \( \frac{288}{360} \) hours, or 0.8 hours.

Holling (1965) showed that \( a \) can be estimated by:

\[
(V)(D)(PR)(PA),
\]

where

\[
\begin{align*}
V & \quad \text{is the velocity of the parasitoid while searching;} \\
D & \quad \text{is the reactive field of the parasitoid, the distance within which prey recognition can occur;} \\
PR & \quad \text{is the probability the prey will be recognized once it is in the parasitoid's reactive field;} \quad \text{and} \\
PA & \quad \text{is the probability of attack once the prey has been recognized.}
\end{align*}
\]

The parasitoid, when searching for hosts, walks along the branch of the tree, tapping its antennae on the foliage. When it touches a larva it stops, taps the larva with its antennae, turns around, and oviposits in the host. Antennae are .0043 meters long and extend to the side of the female (Cox 1928). Thus the reactive field, \( D \), given that search is tactile, is .0086 meters. J.M. McLeod (pers. comm.) has observed similar-sized parasitoids searching for prey in a similar manner and estimates speed of search, \( V \), to be 20 to
90 meters per hour. He also estimates that, for similar parasitoids he has observed, the probability of attack, $PR$, is 0.1 to 0.3. Cox's (1928) description of oviposition indicates that the adult female is persistent in her attack in that she will continue searching for the host even if earlier attempts have failed; I set $PA$ to 1.0.

A feasible range for $a$ can now be defined using Equation 10:

$$
(90)(.0086)(.3)(1.0) = .23
$$

$$
(20)(.0086)(.1)(1.0) = .017
$$

Equation 10 only calculates total parasitoid eggs oviposited per square meter of branch area. Cox (1928) states that, although only one egg is oviposited in each attack, the adult female parasitoid does not discriminate between unattacked and previously attacked hosts. Also, only one parasitoid progeny emerges from each host, irrespective of the number of parasitoid eggs laid in that host. Therefore host larvae parasitized does not equal parasitoid eggs oviposited. I used a competition submodel developed by Griffiths and Holling (1969) to calculate the number of larvae parasitized, given the number of parasitoid eggs oviposited (Equation 9).

The frequency distribution of attacks by individual parasitoids are needed to accurately estimate $k$, the dispersion coefficient of the attack distribution; such data do not exist for *Ascogaster*. I chose a range of $k$ values from 0.5 to 1.5 (J.M. McLeod, pers. comm.).
Survival of parasitoid progeny remains to be estimated. Cox (1928) gives no estimate of this, nor does he report where or how emerged parasitoids exist over the winter. I assumed a constant daily mortality in the range of 0.5% to 1%. Emergence occurs about 270 days before attack the following spring; parasitoid progeny survival rate is therefore 0.07 to 0.26. I know of no field studies which can be used to more accurately estimate this parameter.

A summary of parasitoid population dynamics parameters used in the model is given in Table VI; these values are used in the following analyses unless otherwise specified. The values for search rate, dispersion coefficient, and parasitoid survival rate are means of the ranges identified above.

Avian Predation

The equation used to represent avian predation effects is:

\[ D \sum_{i=1}^{3} \frac{B_i A_i N}{g_i + e^{-c_i N}} \]  

where

- \( g, c, A \) are parameters of "Fujii" functional response form (Mace et al. 1978);
- \( D \) is the number of days budworm is preyed upon;
- \( B_i \) is the number of birds per square meter of
Table VI: Parasitoid dynamics parameters. Values below are used unless otherwise stated.

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Total Time Spent Searching</td>
<td>288 hours</td>
</tr>
<tr>
<td>2. Handling Time</td>
<td>0.8 hours</td>
</tr>
<tr>
<td>3. Rate of Successful Search</td>
<td>0.124 m²</td>
</tr>
<tr>
<td>4. Dispersion Coefficient Of Attack Distribution</td>
<td>1.0</td>
</tr>
<tr>
<td>5. Parasitoid Progeny Survival Rate</td>
<td>0.16</td>
</tr>
</tbody>
</table>
branch.

This form calculates an instantaneous attack rate using the functional response equation, and uses the attack rate in an exploitation equation to approximate depletion of prey through the season (D days). I assumed that all predation losses occurred on large larvae before parasitoid emergence, but that the attack period covered the entire large larval and pupal stage.

Avian predators are assumed to search a volume of foliage; that is, they fly among the tree crowns searching for budworm. Therefore, bird density per square meter of branch changes with changing forest biomass. The eastern spruce budworm model uses total branch surface area for crown volume; I use the same metric to derive B:

\[ B_i = \frac{M_i}{\text{SURF}}, \quad \text{(12)} \]

where

- \( M_i \) is the number of birds per acre; and
- \( \text{SURF} \) is the square meters of branch surface area per acre.

Gage et al. (1970) reported observing no numerical response by the bird complex to changing budworm densities. I therefore used the bird densities given in Holling (unpubl. manus.) for estimates of \( M \).

Functional response data have been collected for some
bird species feeding on eastern blackheaded budworm (Gage et al. 1970, Miller and Mook 1970). On 8 sampling days in each of July and August of 1965, 1966, and 1967 in a stand of mature balsam fir containing approximately 24,000 square meters of branch surface area per acre, birds were shot and their stomach contents analyzed. Simultaneously, the density of blackheaded budworm larvae or pupae in the stands was estimated by sampling a mid-crown branch from 300 trees. Nine bird species were considered sufficiently abundant to consider in their analysis. The raw data give the number of mandibles (from larvae) and cremasters (from pupae) per bird stomach.

I converted these to attacks per bird per day by the following formula from Gage et al. (1970):

\[
K \left( \frac{\text{MAN}}{2} + \text{CRE} \right),
\]

where 

\( K \) is a factor (= 9.14) to convert stomach samples to estimates of consumption in an 8 hour period.

The above uses "successful" attack information (gut contents) to derive "attack" information (number of attacks). The larval and pupal stage of blackheaded budworm
are present for about a month. I have, in this derivation, assumed that attack information over a daily period is, in relative terms, instantaneous when compared to the entire predation period. This may not be valid if the bird population can significantly deplete local budworm populations in less than a single day. I will come back to this assumption below.

The functional response data gathered by Miller and Mook (1970) are presented in Figure 9. I fitted equation 11, scaled to attacks per bird per day, to the data in Figure 9 using non-linear parameter estimation, minimizing the sums of squares of the deviations between the estimated function and the data. The results are shown as the solid line in Figure 9.

The fit is not a good one. It should be noted that the parameter estimates derived using this procedure may be highly biased. The independent variable in Figure 9, budworm density, was not known with certainty, but was estimated with sampling. This is a typical "errors in variables" problem for which the measurement errors in the independent variable will tend to make the response (bird feeding rate) appear independent of it. In this case, the parameter estimation overestimates the rate of effective search (the slope of the ascending limb of the response) and underestimates the maximum attack rate (the asymptote of the response).
Figure 9: Functional response of birds to eastern blackheaded budworm. Points are from Miller and Mook (1970); solid line is fitted curve using Equation 11.
A summary of nominal parameter values for avian predation used in the following analyses is given in Table VII. With these parameters, the maximum daily predation rate in a mature forest with 24,000 square meters of branch surface area is 6% of the budworm population. It is 13.5% in a forest with 10,000 square meters of branch surface area (this is a 10 year old forest in the budworm model). Birds can deplete their prey population quickly in an immature stand. The assumption that daily successful attack information can be used to derive an instantaneous functional response is therefore reasonable for mature forests but becomes more tenuous in younger stands.

3.5 Model Equilibrium Structure

I will now describe the role of particular processes in shaping the equilibrium structure described above. All variables plotted in the figures are per m$^2$ of branch surface area.

3.5.1 The Defoliator

The budworm recruitment curve with all processes included (Figure 10a) has 2 potential stable equilibria; one at very low densities, the other at very high densities, separated by an unstable equilibrium. Avian predation on budworm creates the potential lower stable equilibrium because that equilibrium disappears when avian predation is removed from the model (Figure 10b). The potential unstable equilibrium disappears when all parasitoids are removed from
Table VII: Avian predation parameters for eastern blackheaded budworm model. See Equation 11 for explanation of parameters.

<table>
<thead>
<tr>
<th>PARAMETER</th>
<th>VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Density</td>
<td>10.2/acre</td>
</tr>
<tr>
<td>2. A</td>
<td>11.42</td>
</tr>
<tr>
<td>3. g</td>
<td>9.21</td>
</tr>
<tr>
<td>4. c</td>
<td>.58</td>
</tr>
<tr>
<td>5. Feeding Period</td>
<td>28 days</td>
</tr>
</tbody>
</table>
Figure 10: Recruitment curves for eastern blackheaded budworm. a - all processes included. b - avian predation removed. c - avian predation and parasitism removed. d - with changing parasitoid densities; top line has intra-specific competition removed.
the model (Figure 10c). The dip in the recruitment curve at low budworm densities, therefore, is caused by avian predation and parasitism, while the existence of the lower potential stable equilibrium is caused by avian predation alone.

The upper stable equilibrium disappears when all effects of intra-specific competition (lowered larval survival and adult female fecundity) are removed from the model (top line in Figure 10d). Intra-specific competition creates the upper stable equilibrium for budworm.

However, budworm in the real world, and in the model, are not faced with a constant environment. For example, insect recruitment is dependent upon parasitism rates which are in turn a function of adult female parasitoid density (Equation 9). Changing parasitoid densities changes the position of the recruitment curve (Figure 10d). Increasing parasitoid densities lower the recruitment curve while decreasing parasitoid densities raise it. The effect is most pronounced at low budworm densities because of the depensatory nature of the parasitism process (Section 2.4.1).

An isorecruitment curve of budworm as a function of adult parasitoid density (Figure 11) shows the insect curve has 2 stable surfaces, an upper and lower, separated by an unstable surface; these correspond directly to the appropriate equilibria of Figure 10a.

Two points in Figure 11 will be of interest in further
Figure 11: Budworm isorecruitment curve as a function of parasitoid density. m is maximum parasitoid density for epidemic budworm; n is minimum parasitoid density for endemic budworm.
analyses: point \( m \), the parasitoid density above which the upper stable surface for budworm disappears, and point \( n \), the parasitoid density below which the lower stable surface for budworm disappears.

3.5.2 The Parasitoid

The parasitoid equilibrium structure (Figure 12) has a single stable surface. The bending over of the surface at high parasitoid densities is caused by increasing superparasitism rates with high parasitoid densities (Appendix II), simulated using a competition equation (Griffiths and Holling 1969). The position of the surface is set by the numerical response of the parasitoid to budworm densities and is determined by four parameters (Equation 9): parasitoid fecundity; rate of successful search; parasitoid progeny survival from the time of emergence from the host to the time of attack the following generation; and the dispersion coefficient of attacks. The effects of alternate parameter values on equilibrium structure and model behavior will be discussed in Section 3.10.

3.5.3 The Foliage

The equilibrium structure for the foliage in relation to budworm density (Figure 13) is complicated. There is a stable surface at high foliage biomass (Figure 13a) and a lower stable surface with low branch density (i.e., young forests) which changes into an unstable surface as branch density increases. Foliage equilibrium structure is depen-
Figure 12: Parasitoid recruitment curve as a function of budworm density. The bending of the curve is caused by the competition equation (Appendix II).
Figure 13: Foliage isorecruitment curves as a function of budworm density. a - for three forest types. b - with low, model, and high old foliage natural mortality. c - with low, model, and high new foliage natural mortality.
dent on branch density because it is assumed that budworm do not attack trees less than 21 years old (Jones 1977a). These age classes provide a refuge of full foliage. This refuge forms a large proportion of the total forest foliage when the forest is young but decreases as branch density increases. The dynamics of old foliage (Jones 1977a, p. 109) are the primary processes which create the upper stable surface for foliage in the model (Figure 13b). Changing new foliage dynamics has no observable influence on the foliage equilibrium structure (Figure 13c).

3.5.4 The Forest

The branch area equilibrium structure in relation to foliage biomass contains a single stable surface (Figure 14). The maximum branch surface area is set by the amount of branch surface area at each age (Jones 1977a, p. 103, Figure 14a). The slope of the isorecruitment curve is set by the susceptibility to mortality of the forest (Jones, 1977a, p. 114) (Figure 14b). Lower susceptibility to low foliage levels means that the forest will be able to keep a high branch density with heavy reductions in foliage.

3.6 Processes Which Keep Budworm Chronically Endemic

Eastern blackheaded budworm remains at low population levels for many years in many parts of its range (Canada 1939 to 1982, Miller 1966, Table III). In this section, I will demonstrate the conditions in the model which can give rise to this type of behavior. Such behavior will occur if
Figure 14: Forest isorecruitment curves as a function of foliage density. a - with low, model, and high branch surface area growth rate. b - with low, model, and high susceptibility to mortality from defoliation.
the point n of Figure 11 is moved to the extreme right and past the maximum or minimum value of any variable defining the X axis.

Poor weather conditions, (poorer than that defined as "normal" in the model, Section 3.4.4) low branch density, high parasitoid densities and low foliage biomass can move point n to the far right of the isorecruitment curves (Figure 15) and therefore have the potential to keep budworm numbers endemic. But, the parasitoid density required (about .04/m² branch, from Figure 15c) to keep budworm numbers on the lower stable surface (about 3 budworm eggs/m² branch, point o in Figure 15c) cannot be supported by such, an "endemic" number of budworm (Figure 12), as 3 budworm/m² branch can support only .015 parasitoids/m² branch (Figure 12).

3.7 The Role Of Weather

The preceding section showed that low weather-induced larval survival can make the lower stable surface for budworm, created by avian predation, exist even though other conditions in the model may be favorable for budworm recruitment (e.g., low parasitoid densities). However, normal variation in weather (Section 3.4.4) cannot prevent outbreaks from occurring (Figure 16). If other conditions in the model are favorable for budworm recruitment, both the
Figure 15: Conditions potentially creating chronically endemic budworm populations. a - poor weather induced larval survival. b - low forest biomass. c - high parasitoid densities. d - low foliage biomass. See text for an explanation of point o in 15c.
Figure 16: Budworm isorecruitment curves as a function of foliage biomass with different levels of weather induced larval survival.
lower and upper equilibria disappear, irrespective of weather conditions, and budworm densities can move from endemic to epidemic and from epidemic to endemic levels.

Therefore, the major effect of weather in the model is to delay or advance budworm outbreak formation and collapse which would occur inevitably anyway. Because of this conclusion, all further analyses below will use average weather conditions; the results of the analyses would be the same under any weather condition.

3.8 The Role of Parasitoids

Budworm parasitoids cannot create a stable lower equilibrium density for budworm (Figures 12 and 15c) and keep budworm endemic because sufficient parasitoids cannot be supported by such low budworm populations. Can the parasitoid cause the collapse of budworm outbreaks?

Two sets of isorecruitment curves, one for budworm as a function of parasitoid density, the other for the parasitoids as a function of budworm density, both generated for different foliage levels (Figure 17) show that the parasitoid isorecruitment curves intersect the budworm curves to the left of the prey (i.e., budworm) isorecruitment curve peak. This should therefore cause increasing oscillations (Rosenzweig and MacArthur 1963; Figure 3).

Assuming constant high foliage and branch density for the moment, budworm and the parasitoid begin moving from low
Figure 17: Budworm isorecruitment curves as a function of parasitoid density and parasitoid isorecruitment curves as a function of budworm density for different foliage levels. The system can have trajectory S1 or S2, depending on the parasitoid numerical response. The notation in this figure will be followed throughout Chapters 3, 4, 5. B - defoliator; P - parasitoid; Fo - foliage; F - forest. L - low levels of variable whose density is being varied; M - medium levels; H - high levels.
levels of each. Budworm will begin increasing first, as parasitoids are lagged to budworm by one year (Equation 9).

It is difficult to say what the nature of the behavior of the system will be once it has moved from low budworm and parasitoid levels. Certainly, increased budworm densities will cause some defoliation and shifting of the budworm curves to the right and parasitoid curves downward.

Two extreme possibilities can be envisioned and both are dependent on the relative numerical responses of the budworm and the parasitoid. If the budworm has a more rapid numerical response than the parasitoid the trajectory would likely be S1 in Figure 17. If the parasitoid has a more rapid numerical response than the budworm, the trajectory would likely be S2. The outcomes are likely to be much different under case S1 than S2. A set of foliage isorecruitment curves as a function of budworm density and a set of budworm isorecruitment curves as a function of foliage density illustrate this point (Figure 18) (the foliage isorecruitment curve does not change as a function of parasitized density because no differential feeding between parasitized and unparasitized budworm is assumed).

The upper stable surfaces for budworm and foliage do not intersect; that is, there is no joint equilibrium between budworm and foliage at high levels of each. Under trajectory S1 budworm reach sufficiently high levels so that the upper foliage equilibrium disappears. Under trajectory
Figure 18: Foliage isorecruitment curves as a function of budworm density and budworm isorecruitment curves as a function of foliage biomass with different parasitoid densities.
S2, parasitoids have a sufficiently fast numerical response to stop budworm from reaching levels which would cause the upper foliage equilibrium to disappear. Declines in foliage caused by high budworm densities (Figure 18) would cause high forest mortality and declines in forest branch density (Figure 19).

Whether the system trajectory is S1 or S2 (essentially, whether parasitoids can cause collapse of outbreaks) cannot be determined by simple analysis of equilibrium structure and model simulation must be used. The determining factor is the relative numerical responses of the parasitoid and the budworm. If changes in parasitoid numbers are faster than those of budworm we should expect to see short lasting infestations with little declines in foliage or forest levels. If parasitoids change slowly relative to budworm, budworm infestations should cause large declines in foliage and branch density levels and inter-outbreak periods should be characterized by regeneration of foliage and forest to high levels.

3.9 Temporal Model Behavior

The preceding sections have presented 2 sets of equilibrium structures for the model (Figures 15a and 17 to 19). This section presents the numerical results generated by each set of equilibrium structures.

3.9.1 Temporal Behavior With Chronically Poor Weather

The first equilibrium structure (Figure 15a), should
Figure 19: Forest isorecruitment curves as a function of foliage biomass and foliage isorecruitment curves as a function of forest biomass for different budworm densities.
generate a behavior which is characterized by an absence of outbreaks, continual low parasitoid numbers, and continual high foliage biomass and branch density. This behavior should occur poor weather conditions in the model cause the low density stable equilibrium to remain, irrespective of any other condition.

A simulation of the model made with weather-induced large larval survival set at 0.35 (Figure 20) shows the generated behavior is consistent with that expected from an analysis of equilibrium structure (Figure 15a). There are no budworm outbreaks over a 60 year time span. Parasitoid levels remain low and foliage and forest levels remain high for the 60 year period. This generated behavior has good qualitative correspondence with the behavior of the real world system in some cases (Miller 1966, Canada 1939 to 1982).

3.9.2 Temporal Model Behavior With Normal Weather

I was unable to deduce what behavior the second equilibrium structure (Figures 17 to 19) will generate without actually generating the simulation results. Simulation results generated with model parameters set so as to give the equilibrium structure of Figures 17 to 19 (Figure 21) show budworm outbreaks occurring about every 16 years and lasting 2 to 3 years. Outbreaks cause moderate declines in foliage levels and very little loss of forest biomass. Parasitoid levels reach a peak in the declining phase of
Figure 20: Model behavior for chronically low weather induced larval survival. See Figure 15a for equilibrium structure.
Figure 21: Model behavior under normal weather conditions. See Figures 17, 18, and 19 for equilibrium structure.
budworm outbreaks. This behavior is very much like the behavior of the system in New Brunswick documented by the Forest Insect and Disease Survey (Canada 1939 to 1982) and studied by Miller (1966, Table III). The simulation results also demonstrate that the model parasitoid is able to respond quickly enough to increases in budworm numbers to prevent budworm from reaching even higher levels and inflicting heavy declines of both foliage and forest; that is, it can collapse outbreaks.

A further demonstration that the capability of the parasitoid to quickly respond numerically to host numbers is critical to model behavior is shown in Figure 22. The parasitoid progeny survival was set to .05 for the final 100 years of a 150 year simulation shown in Figure 22. Model behavior in the first 50 years is like that shown in Figure 21. The final 100 years, however, are marked by infrequent but very heavy budworm infestations causing large declines in foliage and forest, a behavior much like that for the unmanaged eastern spruce budworm system (Blais 1968, Table III). The parasitoid numerical response is obviously very critical in determining the behavior of the model.

3.10 Effects Of Alternate Parasitoid Attack Parameters

Many of the parasitoid attack parameters were estimated without any empirical evidence. Minima and maxima for three parameters: rate of successful search; the dispersion coefficient for the distribution of attacks; and the parasitoid
Figure 22: Model behavior for a 150 year simulation with normal weather conditions. Parasitoid progeny survival is that given in Table VI for first 50 years and three times lower for final 100 years.
progeny survival rate (Equation 9) were established. The analyses of the preceding sections were made with averages of the minimum and maximum defined for each parameter. This section tests the sensitivity of the model equilibrium structure and behavior to extreme values of these parameters.

3.10.1 Good Searcher, High Survival, Low Superparasitism

This parameter set increases the capability of the parasitoid to respond numerically. The new parameter set shifts the budworm isorecruitment curves to the right and the parasitoid isorecruitment curves downward in Figure 23a (compare to Figure 17). The effect is to shift the common equilibria farther down to lower budworm levels.

The model behavior generated by this equilibrium structure (Figure 24) is very similar to that for the base model under normal weather conditions (Figure 21). However, outbreaks are less frequent and parasitoid numbers generated from outbreaks are much higher. Both these conditions are generated by the increased numerical response capabilities of the parasitoid.

3.10.2 Poor Searcher, Low Survival, High Superparasitism

This parameter set decreases the ability of the parasitoid to numerically respond to increasing budworm. This has the opposite effect to the parameter set described in the above section (Figure 25, compare to Figure 17 for the "normal" and 23 for the "super" parasitoid). Budworm
Figure 23: Model equilibrium structure for "super" parasitoid. Compare with equilibrium structure in Figure 17.
Figure 24: Model behavior generated with "super" parasitoid. Compare with model behavior in Figure 21.
Figure 25: Model equilibrium structure for "slow" parasitoid. Compare with equilibrium structure in Figure 17 and Figure 23.
isorecruitment curves are shifted to the left and parasitoid isorecruitment curves are shifted upward. The common equilibria are now on the upper stable budworm surface. This means that model behavior should be determined by foliage and forest growth processes as in the last 100 years of model simulation in Figure 22.

The model behavior generated (Figure 26), is what is expected given the equilibrium structure with outbreaks causing large declines in foliage and forest biomass and periods between outbreaks marked by regeneration of foliage and forest.

These last two sets of equilibrium structures and simulations illustrate very clearly the notion that the relative numerical responses of the parasitoid and the budworm are critical in determining the behavior of the model.

3.11 Summary

The analyses in the preceding sections have identified a small set of processes which create the equilibrium structures for individual components of the eastern blackheaded budworm system:

1. avian predation on budworm larvae;

2. effects of intra-specific competition on budworm;

3. parasitoid fecundity, parasitoid progeny survival, rate of successful search, and intra-specific com-
Figure 26: Model behavior generated with "slow" parasitoid. Compare with model behavior in Figure 21.
petition among developing parasitoids caused by super-parasitism;

4. density-dependent foliage growth; and

5. density-dependent forest growth.

In addition, there are a set of processes which determine how the particular equilibrium structures for the system components interact to generate model behavior which is consistent with observed system behavior:

1. weather induced larval survival;

2. the parasitoid attack parameters which define its numerical response to budworm; and

3. the susceptibility of forest branch density to low foliage levels.

The parasitoid attack parameters are most important, for they determine the rate of parasitoid numerical response. Sufficiently rapid parasitoid numerical response generates behavior which is consistent with the observed pattern of outbreaks. Sufficiently slow parasitoid numerical response generates behavior not observed in this system, but found in the eastern spruce budworm system.

The analysis has shown that equilibrium structures for model components are set by specific model processes, and that the configuration and interaction of equilibrium struc-
tures of system components, along with time scales of response by key variables, generate model behaviors which are qualitatively similar to real world behavior under similar conditions (Table III).
4.0 THE EASTERN SPRUCE BUDWORM SYSTEM

Eastern spruce budworm is the major defoliating insect of the eastern coniferous forest of North America. It is found throughout the Canadian Maritimes and northern New England and westward and northward through middle Canada up to the boreal forest (Davidson and Prentice 1967). Its favored host tree species are balsam fir and white spruce. Outbreaks of the budworm have been documented through tree ring analysis back to the 1700's (Blais 1968). Intensive insecticide spraying on the defoliator commenced in many parts of eastern North America in the early 1950's (Prebble 1975) and continues at present.

The behavior of this system has been analyzed exhaustively by a number of workers (Baskerville 1976, Clark 1979, Clark and Holling 1979) using a detailed simulation model of the system (Jones 1977a). The purpose of this chapter is to complement, rather than redo these analyses. Therefore, this chapter contains a description of the real system, a summary of previous workers' analyses of system structure and behavior, and analyses relevant to this thesis which were not carried out by previous workers. The reader is referred to appropriate references for more detailed reports of model structure and behavior.

4.1 Documented Behavior

This system exhibits essentially 3 different types of behavior (Table III). First, there have been no recorded
outbreaks by the budworm in the extreme northern parts of its distribution, although budworm are present there because they can usually be recovered in Forest Insect Survey tree beating samples (Canada 1939 to present).

A second type of behavior is characteristic of the large areas of the system before intensive pesticide application policies were adopted in the early 1950's. This behavior is characterized by irregular infestations occurring every 20 to 90 years over large areas of the host forest (Blais 1954, 1968). These infestations lasted 5 to 11 years in any one site (Miller 1975) and caused very high mortality of mature balsam fir and associated white spruce. Between outbreaks, evidence indicates that the budworm was extremely rare but usually recoverable in tree-beating surveys (Greenbank 1963).

The third type of behavior has occurred in stands either composed mainly of white spruce or subjected to intensive insecticide spraying since the early 1950s (Morris 1958, Blais 1974, Wotton and Jones 1976). This behavior is characterized by long-lasting infestations occurring every 10 to 15 years and causing low or moderate tree mortality.

4.2 System Description

4.2.1 The Defoliator

The life history of the insect is well documented (Morris 1958, Davidson and Prentice 1967, Greenbank 1963). Eggs are laid in the late summer and emerge about 2 weeks
later. Emerging larvae disperse aerially on silk threads, then spin hibernaculae where they diapause over winter. The second instar larvae emerge from diapause in early May. Dispersal occurs again in the same manner as in the fall, whereupon feeding commences on the new foliage of the host tree. Old foliage is consumed if all the new foliage is gone. The insect passes through 4 more instars until early July when the mature larva pupates for about 10 days in the final feeding sites on the host tree. Adults emerge in late July and may disperse. If dispersal does occur, it may extend 10 to 100 kilometers.

4.2.2 Natural Enemies

The budworm is attacked by a large complex of parasitoids on early larvae (Miller 1977). *Apanteles fumiferanae* and *Glypta fumiferanae* are the most important species of the complex (Miller 1959, 1960), being the most completely host-specific and causing the highest mortality rates on the host (Miller 1963). These two parasitoid species attack budworm in the fall, generally after the first larval dispersal, and emerge from the host when the host is in the fifth or sixth larval instar.

Later larval and pupal stages are attacked by a large complex of birds (Morris et al 1958) and evidence indicates that their effect on budworm populations may be greatest at low budworm densities (Morris 1963).

4.2.3 The Forest
A general description of the balsam fir/spruce forest is given in the analysis of the eastern blackheaded budworm/balsam fir system in Chapter 4. Eastern spruce budworm is identical to eastern black-headed budworm in terms of the ages of tree preferred as defoliator habitat and the ages of foliage preferred for feeding.

4.3 Model Description

The simulation model used in my study is described in Jones (1977a). It is a single stand model of the system and has been used as a tool for policy and research design by forest managers and scientists in New Brunswick (Clark et al 1979). The model simulates the annual dynamics of the insect, natural enemies, and host trees in a stand of fir and spruce forest. Many of the interactions simulated between the budworm and its natural enemies and host foliage occur during specific budworm life history stages. There are four major components to the model: the forest, the foliage, the budworm, and budworm natural enemies (birds and parasitoids). The reader is referred to Jones (1977a) and Clark (1979) for a complete model description.

4.4 Model Equilibrium Structure

4.4.1 The Insect

With all processes included, under certain forest conditions budworm can have 2 potential stable equilibria (Figure 27). One is at high budworm densities, the other is at low budworm densities. An unstable equilibrium lies between
Figure 27: Recruitment curves for eastern spruce budworm. 
a - all processes.  b - intra-specific competition effects removed.  
c - parasitism and predation removed.  d - with low, medium, and high foliage biomass.
these 2 stable equilibria. The upper stable equilibrium disappears when intra-specific competition effects (on large larval survival, sex ratio, or fecundity) are removed from the model (Figure 27b). Only the upper stable equilibrium remains with avian predation and parasitism removed from the model (Figure 27c). The unstable equilibrium is created by the saturation of the functional responses of these attacking species.

However, this is a static picture of the model. For example, the budworm recruitment curve depends on foliage biomass through the intensity of intra-specific competition and the survival rate of dispersing larvae (Figure 27d). The position of the curve changes as the foliage density changes, and the position of the equilibria shifts as the position of the recruitment curve changes. Under extreme foliage densities, the equilibria disappear and reappear.

This shifting of equilibria is better captured in an isorecruitment curve (Figure 28). Budworm has an equilibrium structure with an upper and lower stable domain; these correspond to the movement of the upper and lower stable equilibria in response to changing foliage biomass. The unstable domain intermediate to the two stable surfaces corresponds to the unstable equilibrium.

4.4.2 The Parasitoid

The isorecruitment curve for the budworm parasitoid (Figure 29) has one stable equilibrium. The bending over of
Figure 28: Budworm isorecruitment curve as a function of foliage biomass. Point m is the minimum foliage for epidemic budworm; point n is the maximum foliage for endemic budworm.
Figure 29: Parasitoid isorecruitment curves as a function of budworm density. a - low, model, and high fecundity. b - low, model, and high parasitoid progeny survival.
the surface at high parasitoid densities is caused by the increasing super-parasitism rates with high parasitoid densities simulated using a competition equation (Griffiths and Holling 1969) (Appendix II). The position of the curve is set by the parasitoid fecundity, the parasitoid progeny survival from the time of emergence from the host to the time of attack the following generation, and the dispersion coefficient of the competition equation (Appendix II).

4.4.3 The Foliage And The Forest

The foliage equilibrium structure for eastern spruce budworm is the same as that for eastern blackheaded budworm (Figure 13). It contains a lower stable foliage equilibrium at young forest branch area which disappears as the forest grows and an upper stable equilibrium set by the dynamics of old foliage. The appearance of a low density stable surface for foliage at low foliage biomass levels occurs because the younger forest age classes are not fed upon by budworm in the model (Jones 1977a). These younger age classes therefore act as a foliage refuge which disappears under conditions of high forest biomass.

The forest equilibrium structure for eastern spruce budworm is the same as that for eastern blackheaded budworm (Figure 14). The forest equilibrium increases with increasing foliage biomass and the maximum branch surface area is set by the amount of branch surface area at each age (Jones 1977a, p. 103). The slope of the isorecruitment curve is
set by the susceptibility to mortality of the forest (Jones 1977a, p. 113). Lower susceptibility to low foliage levels means that the forest will be able to maintain a high biomass with heavy reductions in foliage.

4.5 Review Of Previous Model Analyses

Clark (1979) and Clark and Holling (1979) concentrated on model analyses which would help explain the two different outbreak behaviors exhibited by the real budworm system in New Brunswick. They therefore concentrated on the interactions between the forest, foliage, and budworm variables, and only examined parasitoid and weather effects only in a cursory manner. I will review the essential points of the previous model analyses and will then turn to a more detailed analysis of the role of the parasitoid and weather.

4.5.1 Model Behavior Under Normal Conditions

We will begin the system at low budworm, high foliage, and high branch surface area. Figure 30 shows that, under normal weather conditions, the lower stable equilibrium for budworm disappears under sufficiently high foliage levels and branch surface area. Under these conditions, budworm begins moving to the upper stable equilibrium. Above about 600 eggs/m², foliage begins to decline very rapidly from its upper stable surface. This decline in foliage levels causes forest branch surface area to begin decreasing as well (Figure 31). The decline in these two variables causes the budworm to move off its upper stable equilibrium and col-
Figure 30: Budworm isorecruitment curves as a function of foliage density and foliage isorecruitment curves as a function of budworm density, for different forest biomasses (Low, Medium, High).
Figure 31: Forest isorecruitment curves as a function of foliage levels and foliage isorecruitment curves as a function of forest biomass, for different budworm levels.
lapse to low levels. This allows both the foliage and, more slowly, the forest to regenerate. This gives a temporal behavior like that shown in Figure 32, with infrequent, long lasting outbreaks resulting in extensive foliage and forest loss. The inter-outbreak period is characterized by regeneration of foliage and forest. This behavior is essentially a defoliator/forest cycle and is similar to the system behavior in the Canadian Maritimes before historical management practices were initiated in the 1950s (Blais 1968, Table III).

4.5.2 Model Behavior With Reduced Forest Susceptibility

A different behavior emerges when the forest is made less susceptible to budworm defoliation, in this case by spraying to reduce budworm populations and maintain high foliage levels to in turn reduce tree and forest mortality. (Figures 33, 34). This has been the forest protection strategy adopted by New Brunswick since the early 1950s (Prebble 1975). A similar equilibrium structure would emerge if the forest were made less vulnerable to defoliation, as is the case with white spruce (Miller 1975). The movement of equilibria described above is the same, except that the movement of the budworm from its upper stable equilibrium is accompanied by declines in foliage but not declines in forest branch surface area. This means that the next outbreak can occur when foliage again reaches high levels but is not delayed by slower forest regeneration. This is essentially a defoliator/foliage cycle (Figure 35) and is
Figure 32: Model behavior for the unmanaged system. The simulation was made with the equilibrium structure described in Figures 30 and 31.
Figure 33: Budworm and foliage isorecruitment curves for different forest biomasses under the historical budworm spray rule. Dotted discontinuities reflect the spray threshold.
Figure 34: Forest and foliage isorecruitment curves for different budworm densities under the historical budworm spray rule. Dotted discontinuities reflect the spray threshold.
Figure 35: Model behavior with historical budworm spray rules. This simulation was made with the equilibrium structure described in Figures 33 and 34. Compare with Figure 32.
characterized by more frequent outbreaks causing usually moderate declines in branch surface area. This behavior is qualitatively similar to that observed by Morris (1958) and Wotton and Jones (1976) on white spruce and to that exhibited by the system under historical insecticide applications (Blais 1974).

4.6 Chronically Endemic Defoliator Populations

The budworm, in many parts of its range, continually remains at low population levels (Table III). This section demonstrates which processes in the model can give rise to this type of system behavior. Endemic for the budworm case is defined as a population which does not cause foliage to decline from its high density stable surface (Figure 18); this is about 600 eggs/m$^2$.

Point n in Figure 18 is the maximum foliage biomass, given the other conditions defining the model, which can keep budworm on its lower stable surface; that is, to keep it from moving from the endemic to the epidemic state. Therefore, any process which moves point n to and past the maximum number of foliage units in the model can keep budworm numbers endemic.

Hypothetically, low forest branch surface area, poor survival of large larvae, and high numbers of adult parasites can each keep budworm populations endemic (Figure 36). Under any of these three conditions, point n disappears, and foliage levels can never become high enough to
Figure 36: Processes potentially creating chronically endemic budworm. a - low forest biomass. b - poor weather-induced larval survival. c - high parasitoid densities. See text for explanation of point o.
permit budworm to move from its lower stable equilibrium.

However, because parasitoid density is a dynamic model variable and because parasitoid populations are coupled to budworm populations in the model, we must make sure that low budworm populations (point o in Figure 36c, about 24 eggs/m²) can sustain the high parasitoid populations needed (about 1 per m² branch surface from Figure 20c) to keep budworm on its lower stable surface. Figure 29, however, shows that the sustainable population of parasitoids is .02 adults/m² from 24 budworm eggs/m². This is far less than that needed to keep budworm endemic (Figure 36c). Parasitoids by themselves are incapable of keeping budworm populations endemic.

The annual reports of the Canadian Forest Insect and Disease Survey (Canada 1939 to 1982) show that areas with chronically endemic budworm contain mature forest with high foliage levels; these conditions in the model cannot keep budworm endemic (Figure 36a). The explicit factor in the model modified in Figure 36b is related to weather influences. This is supported by model simulations (Figure 37), made with very low survival of large larvae, which show an absence of outbreaks and chronically high foliage and forest biomass (the shifts in forest biomass are age-structure effects). The hypothesis, then, is that weather factors inducing poor larval survival are necessary for creating chronically endemic budworm populations.
Figure 37: Model behavior for chronically low weather-induced larval survival. This was made with the equilibrium structure described in Figure 36b. Compare with Figures 32 and 35.
4.7 The Role Of Weather In The Budworm System

Very poor weather conditions can prevent budworm from moving off its lower stable surface (Figure 36b). The effects of normal levels of weather-induced large larval survival (Figure 38) shows that "normal" poor weather (weather-induced survival rates used in the model) cannot by itself prevent initiation of outbreaks if other conditions are appropriate for outbreak initiation; point n does not disappear under normally varying weather conditions. The weather-induced survival rates in the model only have the effect of advancing or delaying initiation of outbreaks that will eventually occur, independent of weather factors.

4.8 The Role Of Parasitoids In The Budworm System

Parasitoids in the model cannot keep budworm populations endemic. The other role which they may have in the model is to collapse an outbreak that has begun.

Two sets of isorecruitment curves, one for the budworm, the other for the parasitoid, for different foliage biomass levels (Figure 39), show that the joint defoliator/parasitoid equilibrium is at the upper stable equilibrium for budworm, at about 2000 eggs/m² of branch. Figure 18 indicates that rapid declines in foliage levels should occur at about 600 eggs/m², and declines in foliage bring about declines in forest branch density (Figure 19). Therefore, before the parasitoid can collapse an outbreak, some very different processes are set in motion to bring
Figure 38: Budworm isorecruitment curves as a function of foliage biomass with different normal levels of weather-induced larval survival. A high forest biomass is assumed.
Figure 39: Budworm isorecruitment curves as a function of parasitoid density and parasitoid isorecruitment curves as a function of budworm density, with different foliage levels.
about this collapse. The parasitoid has too slow a numerical response to be important in the dynamics of the model budworm system.

4.9 **Summary**

The analyses in the preceding sections have identified a small set of processes which create the equilibrium structures for individual components of the eastern spruce budworm model:

1. avian predation on budworm larvae;

2. effects of intra-specific competition on budworm survival and fecundity;

3. parasitoid fecundity, parasitoid progeny survival, and intra-specific competition among developing parasitoids caused by super-parasitism;

4. density-dependent foliage growth; and

5. density-dependent forest growth.

In addition, there is a set of processes which determine how the particular equilibrium structures for the system components interact to generate model behavior which is consistent with observed system behavior:

1. weather induced larval survival;

2. the parasitoid attack parameters which define its
numerical response to budworm; and

3. the susceptibility of forest branch density to low foliage levels.

The analysis has shown that equilibrium structures for model components are set by specific model processes, and that the configuration and interaction of equilibrium structures of system components, along with time scales of response by key variables, generate model behaviors which are qualitatively similar to real world behavior under similar conditions.
5.0 THE JACK PINE SAWFLY SYSTEM

The jack pine sawfly is a native defoliating insect of the eastern boreal forest of North America. It is found wherever jack pine, *Pinus banksiana* (Lamb.), occurs, primarily in Ontario and Quebec. The sawfly is the major pest of jack pine, and will not survive on other host trees (McLeod 1970).

5.1 Documented Behavior

The system exhibits essentially three types of behavior (McLeod 1970 1977a, Table III). First, over large areas of jack pine forest, outbreaks never occur and the insect is never an economic concern. The insect can often be recovered in Forest Insect Survey samples in these areas (Canada 1939 to present). These low sawfly numbers, of course, inflict little defoliation and the host forest grows largely unaffected by the presence of the sawfly (Canada 1939 to present; McLeod 1970). This type of behavior also occurs in immature jack pine forests, as sawfly outbreaks are extremely rare in young jack pine stands (McLeod, pers. comm.).

Second, in some stands of jack pine, sawfly numbers become sufficiently high to cause heavy defoliation and some reduction of tree growth every 8 to 10 years. Tree mortality is rare. High sawfly populations persist for a maximum of 3 years, then collapse. McLeod (1977a) found that, between these outbreaks, the sawfly causes minor defoliation
of the upper crowns of the dominant pine trees in stands.

Third, in very rare cases, sawfly numbers reach extremely high levels. These very high populations remove much of the foliage from the host trees and inflict very heavy tree mortality. Whole stands of mature jack pine are lost and, unless fire releases the seed crop, are not replaced. Sawfly populations collapse once tree defoliation becomes high (McLeod 1977a).

5.2 System Description

5.2.1 The Defoliator

The life history of jack pine sawfly is well documented (McLeod 1968). The insect is univoltine; adult emergence commences in the early spring from puparia that have overwintered in the ground. Adult dispersal is minimal, as the female is a very poor flier. Larvae develop through 4 instars. There is no larval dispersal. Larvae feed on foliage produced in previous years first, but will consume the current year's foliage supply if the old foliage supply becomes depleted. Once feeding is finished in the early fall, larvae drop from the foliage to the ground to pupate; the pupal stage lasts for about 9 months.

Weather is a strong determinant of larval survival. Tripp (1965) found that sufficiently cold temperatures in the late summer and fall will slow completion of larval feeding.
5.2.2 Natural Enemies

A large complex of parasitoids has been recovered from the sawfly (McLeod 1975). The most important species attack large larvae in late summer and emerge from the pupal stage in the spring shortly before adult emergence begins.

The sawfly is preyed upon by primarily 3 guilds of vertebrate predators. Small nesting birds consume the sawfly while they are in the large larval stage and large flocking birds prey on adult sawfly following adult emergence in the late spring (McLeod 1974). Finally, small mammals, primarily the common shrew, *Sorex cinereus cinereus*, prey on the sawfly during its 9 month pupal stage (McLeod 1966).

5.2.3 The Forest

Jack pine stands are fire-originated and therefore are largely of a single or a very few age classes (Rowe 1971). Jack pine retains 4 years of foliage growth (McLeod 1977a). Jack pine grows best on poor sandy soils and is outcompeted on richer sites. Young stands grow very quickly, and stagnation of the stand begins to set in very early, at about 35 years, with declining volume and tree vigor. If left undisturbed, jack pine is slowly replaced by climax black spruce (Rudolph 1958).

5.3 Model Description

The simulation model I used in the following analyses is described in McLeod (1977a, 1977b); a detailed monograph
about the system is currently being prepared (McLeod, in prep.). The simulation model represents a synthesis of a 19 year research program on the system in northern Quebec.

5.3.1 Spatial and Temporal Characteristics of The Model

The model simulates system dynamics on a uniform stand of jack pine forest. Forest and foliage dynamics are simulated once a year, while insect development and many of the processes affecting sawfly dynamics occur during specific sawfly instars.

5.3.2 Forest Dynamics

A single age class of tree is simulated from the time of fire initiation. There is no simulated regeneration of the forest with other tree species. Stand basal area is used in the model as a surrogate for avian predator habitat and as an index of potential foliage development.

There are baseline age-dependent tree survival and diameter growth rates which change stand basal area through time. These baseline rates are modified downward with the level of budworm feeding, measured as the percent defoliation of all foliage.

5.3.3 Foliage Dynamics

Four foliage age classes are maintained and are measured in basal area units. The number of units of new foliage produced in a year is equal to the basal area of the stand. All foliage greater than four years old is dropped
from the tree.

5.3.4 Defoliator and Natural Enemy Dynamics

The major processes in the model which influence sawfly populations are:

1. intra-specific competition for foliage resources;
2. predation, modelled using Type III functional responses, by birds on large larvae and adults;
3. predation, modelled using a Type III functional response, by small mammals on pupae;
4. parasitoid attack on large larvae and parasitoid emergence from fully-developed pupae; and
5. weather influences modelled as a lognormally distributed random variate acting on young larvae.

The following description will be important for the discussions later in the chapter.

Larvae consume old foliage first, without preference for any of the three old foliage age classes. Larvae make up residual foliage demand on new foliage if necessary. Large larval survival and adult female fecundity is linearly proportional to the fraction of foliage demand that is met during feeding.

It is assumed that birds search the tree crowns for
sawfly larvae and adults, so that avian predation is simulated on a tree volume basis. On the other hand, because small mammals search the forest floor for sawfly pupae, small mammal predation is simulated on an areal basis.

Finally, parasitoids attack the last instar larvae and emerge from the pupae just before adult emergence. In the model, parasitoid attack is simulated after larval starvation mortality (if any) has been applied, before avian predation on larvae is simulated. Parasitoid emergence occurs after small mammal predation is calculated.

In the figures used in the following analyses, sawfly and sawfly parasitoid populations are expressed in numbers/m² of ground, foliage is expressed in foliage units, and forest basal area is expressed in square meters/hectare.

5.4 Model Equilibrium Structure

5.4.1 The Defoliator

A sawfly recruitment curve with all model processes included and other variables held constant (Figure 40a) has 3 potential stable equilibria; each pair is separated by a potential unstable equilibrium. The lowest potential stable equilibrium disappears when avian predation is removed from the model (Figure 40b), the uppermost potential stable equilibrium disappears when the effects of intra-specific competition on larval survival and adult female fecundity are removed (Figure 40c), and the middle potential stable equilibrium disappears when small mammal predation on sawfly
Figure 40: Recruitment curve for jack pine sawfly. 
a - All processes included.  
b - Avian predation and parasitism removed.  
c - Intra-specific competition effects removed.  
d - Small mammal predation removed.
pupae is removed (Figure 40d). Therefore, as with both previous models, avian predation creates the potential for a stable equilibrium at very low densities, and effects of intra-specific competition create the potential for a stable equilibrium at very high densities. In addition, small mammal predation creates the potential stable equilibrium for sawfly at intermediate densities.

Avian predation on sawfly in the model is closely coupled to forest maturity as measured by stand basal area. The equilibrium structure for the sawfly changes with changing basal area of stands (Figure 41), and this effect is most extreme at low sawfly densities, where avian predation has its greatest effect.

The effect of changing forest biomass on sawfly equilibrium structure is more easily pictured in an isorecruitment curve (Figure 42). An isorecruitment curve for the model with all processes included has 3 stable surfaces separated by unstable surfaces. There is a direct correspondence between the equilibria of Figure 40a and the domains of Figure 42. Points k and l, under the conditions used to generate this isorecruitment curve, represent the minimum basal area for which the 2 uppermost stable surfaces remain, and points m and n represent the maximum basal area for which the 2 lowermost stable surfaces remain. These points will be used in the analyses below.

5.4.2 The Parasitoid
Figure 41: Recruitment curve for jack pine sawfly for low to high forest biomass, represented by basal area.
Figure 42: Sawfly isorecruitment curve as a function of forest basal area. Points k and l are the minimum basal areas for which sawfly can remain on the uppermost stable surfaces. Points m and n are the maximum basal areas under which sawfly can remain on the lowermost stable surfaces.
The parasitoid has a single stable domain (Figure 43). The equilibrium parasitoid density increases as host density increases. This is caused by increasing super-parasitism rates with high parasitoid densities (Appendix II). The position of the isorecruitment curve is set by the numerical response of the parasitoid to budworm densities and is determined by four parameters: parasitoid fecundity; rate of successful search; parasitoid progeny survival from the time of emergence from the host to the time of attack the following generation; and the dispersion coefficient of the negative binomial distribution describing the degree of super-parasitism (Appendix II).

5.4.3 The Foliage

Foliage has a single stable domain (Figure 44) and the equilibrium foliage biomass at low sawfly densities (the foliage biomass in a jack pine forest without sawfly) increases with increasing basal area of stands. Very simply, foliage biomass in stands without defoliation increases with increasing forest maturity. Significant foliage decline occurs at a defoliator density of about 300 sawfly eggs/m².

5.4.4 The Forest

Like foliage, the forest also has a single stable equilibrium (Figure 45). Forest decline from defoliation begins to occur if foliage biomass decreases below about 350 units per hectare.
Figure 43: Parasitoid isorecruitment curve as a function of sawfly density. See Section 5.5 for an explanation of points o and p. a - changing parasitoid fecundity. b - changing parasitoid search rate. c - changing survival rate of parasitoid progeny.
Figure 44: Foliage isorecruitment curves as a function of sawfly density with high, model, and low forest basal area.
Figure 45: Forest isorecruitment curve as a function of foliage biomass.
5.5 Model Conditions Which Keep Sawfly Chronically Endemic

Section 5.2 outlined 2 observed conditions which keep sawfly endemic. First, young forests never experience sawfly outbreaks (McLeod 1970). Second, extremely poor weather conditions slow larval development in extreme parts of the insect's range (Tripp 1965).

Isorecruitment curves (Figure 46) show that the model produces both these situations. First, the lowest stable equilibrium exists under conditions of low stand basal area. Second, sufficiently poor early larval survival, even in a forest with a high basal area which would ordinarily be able to generate an outbreak, moves point n (see Figure 42) to the far right of the graph and past the maximum possible stand basal area.

Sufficiently high parasitoid levels can also move point n past the maximum possible stand basal area and therefore potentially keep sawfly populations chronically endemic (Figure 47a). However, unlike the budworm models, low foliage biomass does not move point n past the maximum possible forest biomass (Figure 47b). Low foliage levels in this model, then, cannot potentially keep sawfly chronically endemic.

As in the previous models, the question remains whether, in a mature forest, the number of parasitoids required (the rightmost curve in Figure 47a, about .07 adults/m²) to keep sawfly chronically endemic (endemic is
Figure 46: Sawfly isorecruitment curves as a function of basal area with normal to extremely poor early larval survival.
Figure 47: Sawfly isorecruitment curves as a function of basal area.  

- **a** - With different adult parasitoid densities.  
- **b** - With different foliage biomass levels.
about 3.2 eggs/m², from Figure 47a) can be supported by that density of sawfly. Figure 43a shows that only about .012 adult parasitoids/m² (point p) can be supported when the sawfly density is 3.2 sawfly eggs/m² (point o). Parasitoids, then, cannot keep sawfly endemic. The result of this analysis show that low stand basal area and low weather-induced early larval survival are the two conditions in the model which can keep sawfly populations chronically endemic.

5.6 The Role Of Weather

The preceeding analysis showed that very poor weather-induced larval survival can remove any possibility of the sawfly having upper equilibrium (i.e. outbreak) densities (Figure 46). Normal variation in weather (Figure 48) shifts the sawfly isorecruitment curve to the left and right of the curve for normal weather conditions, but the lower stable equilibrium never disappears. Therefore, normal weather variation in the model can advance or delay major shifts in sawfly populations but it cannot cause those shifts. The results of this analysis means that weather effects can be ignored in any remaining model analyses and that constant normal weather conditions will be used in the following analyses. The results would be the same under any normal fluctuation in weather effects.

5.7 The Role Of The Parasitoid

Section 5.5 demonstrated that the parasitoid could not keep sawfly chronically endemic (Figures 43, 47). There
Figure 48: Sawfly isorecruitment curves as a function of basal area with normal variation in weather-induced early larval survival.
remains the possibility that the parasitoid can bring sawfly to endemic levels once it has moved off its lower stable equilibrium.

An overlay of sawfly and parasitoid isorecruitment curves for different foliage levels (Figure 49) shows that the curves intersect just where the lowest unstable curve (set by the declining mortality from avian predation) becomes the middle stable curve (set by small mammal predation). The common equilibrium does not shift with changing foliage levels because the parasitoid attacks sawfly after sawfly has consumed foliage and suffered any starvation mortality.

Significant decline in foliage begins to occur above about 300 sawfly eggs/m²; this is only slightly above the sawfly density at the common parasitoid/sawfly equilibrium (Figure 49). Furthermore, moderate declines in foliage can cause very large declines in forest levels (Figure 45). The parasitoid numerical response is crucial in determining the behavior of the model.

The behavior of the model would likely be very different with different parasitoid numerical responses. With a slow parasitoid, sawfly would increase to the upper equilibrium defined by food limitation (about 2000 eggs/m²; Figure 49). Once sawfly reach about 300/m², foliage biomass begins to decline very quickly (Figure 44) and declining foliage levels create very quick declines in stand basal
Figure 49: Sawfly isorecruitment curves as a function of parasitoid density and parasitoid isorecruitment curves as a function of sawfly density for different foliage levels.
area (Figure 45). Therefore, a slow parasitoid in the model would permit higher outbreak sawfly populations and cause heavy declines in foliage biomass and forest basal area. The decline in foliage biomass would remove the upper equilibrium (Figure 49b) and sawfly would decline to its lowest stable equilibrium. The process determining the periodicity of defoliator populations would be the rate of forest growth in that another infestation could not be generated until a new forest had regrown. The behavior suggested by the equilibrium structure with a slow parasitoid is much like the second type of system behavior described in Section 5.1.

On the other hand, a parasitoid with a rapid numerical response would cause tight cycling around the common equilibrium (Figure 49). This would cause little declines in foliage and forest. In this case, system behavior would be determined by the parasitoid numerical response.

The rate of numerical response of the parasitoid cannot be induced from simple examination of isorecruitment curves. If the parasitoid has a rapid numerical response, foliage and forest declines from peak budworm populations should be minimal. This behavior would be much like the second type of system behavior described in Section 5.1. However, I must resort to model simulation to find out the type of numerical response the parasitoid has and, therefore, which behavior the model will exhibit with a normal parasitoid.
We have reached the limits of the analysis possible using equilibrium structure alone. The following sections examine the behavior generated from the model.

5.8 Temporal Model Behavior

5.8.1 Chronically Poor Weather Conditions

Figure 46 showed that very poor early larval survival could keep sawfly numbers at a lower stable equilibrium and therefore endemic. Model behavior under this condition (Figure 50) shows that sawfly numbers do remain endemic. The initial years of endemic sawfly populations are generated because of the low forest biomass (Figure 46). Endemic sawfly remain endemic in spite of the high forest biomass (Figure 50d) because of the poor weather-induced early larval survival. The chronically endemic sawfly populations allow for unhindered foliage and forest growth (Figure 50c,d). This behavior is very similar to observed behavior of the system in many parts of its range (Table III, McLeod 1970), especially in extreme northern areas (Tripp 1965).

5.8.2 Normal Weather Conditions

Under normal weather conditions, the model can generate 2 different behaviors, depending upon the parasitoid numerical response. Figure 51 shows the model behavior when the parasitoid has a fast numerical response to sawfly after the sawfly's lowest stable equilibrium has disappeared due to high stand basal area. The system oscillates around the
Figure 50: Model behavior with chronically poor weather-induced early larval survival.
Figure 51: Model behavior with normal variation in weather-induced early larval survival.
common defoliator/parasitoid equilibrium of Figure 49. Sawfly outbreaks are generated about every 8 to 10 years (Figure 51a); these outbreaks cause some decline in foliage levels (Figure 51c), but very little decline in forest biomass (Figure 51d). Parasitoid numbers oscillate with changes in host levels with a 1 year lag (Figure 51b). This behavior generated by the model is very similar to the common behavior of the system when the sawfly does exhibit outbreaks (Table III, Section 5.1, McLeod 1977a).

The behavior generated by the model with a slower parasitoid (Figure 52, made with a parasitoid progeny survival rate which is 50% of normal), contains a single massive sawfly outbreak when the forest basal area becomes high enough for the lowest stable equilibrium to disappear (Figure 46). This large outbreak causes heavy loss of foliage and subsequent declines of forest (Figures 52c,d). Parasitoid numbers remain very low throughout the simulation (Figures 52b). This behavior is very similar to the rare type of behavior (Table III, Section 5.2, McLeod 1977a, Canada 1939 to present).

Conditions for producing massive outbreaks in the real system have not been documented. My analysis suggests that some event may have adversely affected the parasitoid population and reduced its effectiveness in some way, since the only way to generate this type of behavior in the model is to slow the parasitoid numerical response to prevent cycling around the joint parasitoid-sawfly equilibrium.
Figure 52: Model behavior with parasitoid progeny survival at 50% of normal and normal variation in weather-induced early larval survival.
5.9 A Fourth Type of Behavior

The reason for the collapse of foliage biomass and forest basal area from a massive sawfly outbreak (when the model parasitoid is made slow) is that the forest is sensitive to loss of foliage (Figure 45). Forest basal area declines very quickly with only moderate loss of foliage. In this section, I will alter the equilibrium structure of the forest to generate another type of model behavior.

I altered the model functions relating defoliation to reduction in radial growth and increase in tree mortality, so that more defoliation was needed to create growth and mortality effects. This, in effect, makes the jack pine less vulnerable to mortality from a given level of defoliation. This modified the forest equilibrium structure as shown in Figure 53 (compare to Figure 45); a very large decline in foliage biomass is now needed to decrease the stable forest basal area.

The equilibrium structure now defined by Figures 42, 44, and 53 is different to any previously defined. Given a mature forest, the lowest stable equilibrium for sawfly disappears, leaving the defoliator free to increase to the upper stable equilibrium (the parasitoid is assumed again to have a slow numerical response). Foliage levels begin to decline very quickly once sawfly increase to about 300/m², and the stable foliage level is extremely low once sawfly reach their upper equilibrium. But, forest basal area
Figure 53: Forest equilibrium structure with lowered vulnerability to defoliation. Compare with Figure 45.
remains high over a large range of foliage biomass (Figure 53). The uppermost equilibrium for sawfly disappears with sufficiently low foliage levels, and these low foliage levels generated by high sawfly in turn collapse the sawfly population. The middle stable equilibrium remains under low foliage conditions and sawfly densities should decrease to this level. Stand basal area should still be high at the end of the outbreak, and the low (relatively) sawfly densities and still high basal area should allow the foliage levels to recover (Figure 44). Sawfly numbers should increase once again after foliage levels have regenerated.

The picture that emerges from this equilibrium structure is that model behavior is set by the recruitment and dynamics of foliage. The behavior that should result should be one where the defoliator population moves from the middle stable equilibrium to the upper stable equilibrium and back with the growth and decline of foliage. Because the parasitoid has a slow numerical response to sawfly, they should remain at low levels throughout the simulation.

This is exactly the behavior generated by the model (Figure 54). Movement of sawfly populations from 300 eggs/m² to higher levels appears to occur at intervals of about 10 years. These cause large declines in foliage, but little to moderate decline in forest basal area.

The periodicity of outbreaks in this situation is very similar to that in the fast parasitoid case (Figure 51).
Figure 54: Model behavior with parasitoid progeny survival at 50% of normal, normal variation in weather-induced early larval survival, and reduced forest vulnerability to defoliation.
The evidence from existing long term sawfly population data (Table III, Appendix I) suggests that the 6 to 10 year outbreak period is determined by a fast parasitoid. Model results suggest that, if the 6 to 10 year outbreak period is determined by a defoliator/foliage cycling, sawfly populations would regularly reach greater than 1000 eggs/m² and that the population would rarely drop below about 300 eggs/m² (Figure 54). However, if the 6 to 10 year outbreak period is determined by a defoliator/parasitoid cycling, sawfly populations would reach 300 eggs/m² during outbreak peaks and would decline to less than 100 eggs/m² between outbreaks. The jack pine sawfly data in Appendix I show that the latter is a more realistic description of the defoliator population behavior.

But, this fourth type of behavior does indicate that defoliator/foliage cycling may produce qualitative behaviors that are difficult to distinguish from behaviors generated by defoliator/parasitoid cycling on the basis of defoliator population behavior alone. I will return to this issue in development of the integrative theory in Chapter 6.

5.10 Summary

The analyses in the preceding sections have identified a small set of processes which create the equilibrium structures for individual components of the jack pine sawfly system:
1. avian predation on sawfly larvae and adults;

2. effects of intra-specific competition on sawfly survival and fecundity;

3. parasitoid fecundity, parasitoid progeny survival, rate of successful search, and intra-specific competition among developing parasitoids caused by super-parasitism;

4. density-dependent foliage growth; and

5. density-dependent forest growth.

In addition, there is a set of processes which determine how the particular equilibrium structures for the system components interact to generate model behavior which is consistent with observed system behavior:

1. weather induced larval survival;

2. the parasitoid attack parameters which define its numerical response to sawfly; and

3. the susceptibility of forest branch density to low foliage levels.

The parasitoid attack parameters are most important, for they determine the rate of parasitoid numerical response. Sufficiently rapid parasitoid numerical response generates behavior which is consistent with the observed
common pattern of outbreaks (Figure 51). Sufficiently slow parasitoid numerical response generates behavior rarely observed in this system (Figure 52).

The analysis has shown that equilibrium structures for model components are set by specific model processes, and that the configuration and interaction of equilibrium structures of system components, along with time scales of response by key variables, generate model behaviors which are qualitatively similar to real world behavior under similar conditions.
6.0 THE INTEGRATIVE THEORY

6.1 Introduction

The detailed analysis of the structure and behavior of three defoliating insect models in Chapters 3 to 5 showed that the models mimic well the qualitative behavior of the systems they represent (Table III). This chapter integrates these analyses, with pertinent observations presented in Table III, into a general theory of the structure and behavior of defoliating insect systems. Before developing this theory, it is worthwhile to reiterate the objectives of this thesis:

1. define a set of components, or state and driving variables which are necessary and sufficient to predict the qualitative properties of defoliating insect system behavior;

2. collapse the plethora of defoliating insect system behaviors into a small set of classes, each identified by characteristic temporal properties of the components;

3. show how the classes of behavior can be deduced from a set of key interactions among the components;

4. show that the state components each exhibit one of a small number of different equilibrium structures; and
5. show that the key interactions among the components which determine system behavior and the equilibrium structures of the components in any defoliating insect system can be predicted with a minimum set of information about the components themselves.

Each objective above will be dealt with in a separate section below.

6.2 Elements Of Observed Behavior Not In Model Analyses

There are important elements of Table III which were not a part of any of the detailed system analyses of Chapters 3 to 5 and which have to be considered in the development of the integrative theory. The most obvious one is the fact that the outbreaks in many of the systems described in Table III are terminated by disease epizootics but disease is not a variable in any of the three systems analyzed in the previous three chapters. In truth, defoliator diseases occur in all defoliating insect systems. They happen to be unimportant in determining the behavior of the three systems I analyzed in detail. I will have to rely on work of other scientists in order to incorporate disease into the integrative theory. The temporal behavior of the systems in which disease epizootics have been observed to terminate defoliator outbreaks is very similar to the temporal behavior of those systems in which parasitism has been observed to terminate outbreaks. I will therefore assume
that the behavior of systems in which disease terminates outbreaks will be the same as the behavior of systems in which parasitoids terminate outbreaks.

Also, it is not clear whether defoliating insect system behavior set by a defoliator/parasitoid cycle can always be distinguished from one which is set by a defoliator/foliage cycle (see Chapter 5). This issue will be discussed in Section 6.5.3.

The major elements of the integrative theory are presented in boldface below.

6.3 System Components

The essential qualitative properties of defoliating insect system behavior can be captured with variables representing the dynamics of the defoliator, the forest, the foliage, the parasitoid, and the disease, and a variable representing the effect of weather on the defoliator.

The three models analyzed in Chapters 3 to 5 were constructed with a minimum number of state variables required to represent the dynamics of the systems: the defoliator density, the forest biomass or level of maturity, the foliage biomass, and the parasitoid density. In addition, Table III indicates that disease is often an important determinant of behavior. A driving variable, representing weather effects on defoliator survival, completes the list of components. The simulation of the 5 state variables plus the effects of a driving variable simulating weather-induced defoliator mortality, and a set of processes defining
interaction among them, can capture the essential qualitative properties of defoliating insect systems.

6.4 Classes of Behavior

There are 4 qualitatively different classes of defoliating insect system behavior.

In all the behaviors generated by the 3 models, 4 distinct classes can be identified (Figure 55).

6.4.1 Class 1: Chronic Endemic

This class of behavior is characterized by an absence of defoliator outbreaks with no visible defoliation or forest mortality. The eastern spruce budworm, eastern black-headed budworm, and jack pine sawfly models and systems exhibit this behavior, as do probably most defoliating insect systems in some parts of their range.

6.4.2 Class 2: Defoliator/Parasitoid-Disease Cycle

This class of behavior is characterized by short duration, frequent defoliator outbreaks with high parasitism or disease mortality rates in the decline phase of outbreaks. Foliage and forest biomass are largely unaffected by insect levels during outbreaks. The jack pine sawfly and eastern black-headed budworm models and systems exhibit this behavior.

6.4.3 Class 3: Defoliator/Foliage Cycle

This class of behavior is characterized by periodic outbreaks causing large declines of foliage but relatively
Figure 55: The 4 classes of insect/forest system behavior, shown in stylized fashion.
small declines in forest biomass. This behavior was generated in the eastern spruce budworm/balsam fir spruce and the jack pine sawfly/jack pine models and has been observed in the eastern spruce budworm system in pure stands of white spruce.

6.4.4 Class 4: Defoliator/Forest Cycle

This class of behavior is characterized by long-lasting infestations occurring with low frequency. Infestations cause large declines in foliage and forest basal area and both recover to high levels between outbreaks. This behavior was generated in all models.

6.5 Processes Determining System Behavior

The particular class of behavior a system exhibits is determined by weather effects on defoliator survival, the speed of the parasitoid numerical response, the speed of the disease numerical response, and the sensitivity of the forest to low foliage levels.

The behavior of any particular defoliating insect system is determined by a small set of processes.

6.5.1 Class 1 Behavior

Class 1 behavior is associated in the models with high defoliator mortality from weather effects which maintains a below-outbreak stable equilibrium density for the defoliator (Figures 15, 36, 46).

6.5.2 Class 2 Behavior

This behavior in the models is associated with normal
rates of weather-induced larval survival and a parasitoid which has a rapid numerical response to changes in defoliator densities, relative to defoliator recruitment. The temporal patterns of behavior in this class occur because of the interaction between the fast variable, the defoliator, and another fast variable, the parasitoid or the disease. The periodicity of behavior is set by the numerical response of the parasitoid or disease. The parasitoid or disease is a sufficiently fast variable that the foliage or forest equilibrium structure has no influence on the temporal behavior.

6.5.3 Class 3 Behavior

This behavior in the models is associated with normal rates of weather-induced defoliator survival, a slow parasitoid and disease (relative to the defoliator), and a forest which is invulnerable to declines in foliage biomass. The periodicity of events is determined by the growth and replacement of the foliage variable. This means that the temporal pattern of this behavior will be indistinguishable from that of a Class 2 system for particular foliage recovery times and implies that simply examining the outbreak frequency is insufficient to determine what class of behavior the system is exhibiting. The parasitoid and disease are sufficiently slow variables that they have no influence on system behavior. The forest variable is insensitive to loss of foliage and therefore also does not influence the behavior of the system.
6.5.4 Class 4 Behavior

This behavior is associated with normal levels of weather-induced larval survival, a slow parasitoid and disease (relative to the defoliator), and a forest which is vulnerable to declines in foliage levels. The behavior is determined by the interaction of the the defoliator and the forest. The parasitoid and disease variables are too slow to have any influence on system behavior, and the sensitivity of the forest variable to low foliage levels means that the periodicity of events is set by the growth and replacement of the forest.

6.6 Information Required To Predict System Behavior

6.6.1 Weather Effects

Weather effects can be predicted by knowing comparative defoliator developmental rates

Weather conditions will invariably cause some mortality to the defoliator. It is the amount of mortality that weather factors inflict which determines whether a Class 1, Class 5, or some other behavior will result. Weather-induced reduction in larval survival shifts the isorecruitment curves, whatever their configuration may be, such that only the lowest stable equilibrium remains.

The effects of weather on defoliator survival may be estimated using indices such as comparative developmental rates (Tripp 1965).

6.6.2 Parasitoid Numerical Response
The speed of the parasitoid variable can be predicted by knowing the life stage of the host attacked, the distribution of attacks, the rate of effective search, the progeny survival rate, and the defoliator recruitment.

**Parasitoid Fecundity**

Parasitoid fecundity can be determined if the life history stage of the defoliator that is attacked is known. This is because Price (1975), in an extensive analysis of parasitoid fecundity data, found a very good correlation and significant regression between parasitoid fecundity and the life history stage of the host attacked.

**Distribution of Attacks**

The dispersion coefficient of the distribution of attacks is also relatively simple to estimate with short laboratory or in-situ field studies of parasitoid egg distribution in hosts which have been attacked by a single parasitoid. This has been done for a number of important parasitoids in a number of defoliating insect systems such as *Apantales fumiferanae* and *Glypta fumiferanae* on eastern spruce budworm (Miller 1959) and *Pleolophus basizonus* on European pine sawfly (Griffiths and Holling 1969).

**Rate Of Effective Search**

Holling (1965 1966) has shown that the rate of effective search can be estimated from a number of behavioral attributes of the searching parasitoid: speed of search; reactive distance; probability of detection given the host enters the parasitoid's reactive field; and the probability
of attack given detection. These procedures were used to estimate the rate of effective search for the eastern black-headed budworm parasitoid using simple behavioral information about the parasitoid (Chapter 3). Field estimation of this parameter may be more difficult than laboratory estimation because of the problems involved in observing the attack behavior of parasitoids under field conditions (J.M. McLeod, pers. comm.).

Parasitoid Progeny Survival

The estimation of parasitoid progeny survival is likely to be time-consuming. Its estimation requires detailed field studies to derive parasitoid life tables, or at least, survivorship curves.

In addition, this information must be coupled with defoliator life table or survivorship studies designed to estimate defoliator recruitment. Once all this is known, the parasitoid recruitment can be compared to the defoliator recruitment to determine the speed of the parasitoid variable relative to the speed of the defoliator variable (Huf-faker et al. 1977).

6.6.3 The Disease

The speed of the disease variable can be predicted by knowing disease pathogenicity, length of the infective stage, and defoliator recruitment

Disease was not a part of any of the three systems analyzed in detail. However, Anderson(1979) and Anderson and May (1980) have found that diseases which have a high
pathogenicity, defined as high host mortality rate from infection, and a long-lived infective stage are capable of creating epizootics. Therefore, I will define these factors as the minimum set of information necessary to determine the speed of the disease variable. As with the parasitoid variable, however, defoliator life table or survivorship studies must also be conducted to determine the speed of the disease variable relative to that of the defoliator.

6.6.4 Forest Vulnerability To Defoliation

Forest vulnerability to defoliation can be predicted by knowing the tree mortality rate for a range of defoliation rates at the time defoliator feeding occurs.

This can be gathered using either artificial defoliation (Craighead 1940) or defoliation by the insect (Wickman 1978). It is important that the artificial defoliation experiments be done during the season that the defoliator consumes most of its ration. Craighead (1940), for example, found that the timing of foliage removal was critical in determining whether a tree lived or died.

6.7 Alternate Structures And Necessary Information

6.7.1 The Defoliator

The defoliator can exhibit one of four different equilibrium structures, and the defoliator equilibrium structure is determined by the presence, absence, and form of predation by crown-searching predators, primarily birds, predation by ground-searching predators, primarily small mammals, and intra-specific competition.

Intra-specific Competition

Intra-specific competition always occurs and
creates a stable equilibrium at a high defoliator density

Intra-specific competition occurs in all 3 models and creates a stable surface in all defoliator isorecruitment curves at high densities (Figures 10, 27, 40). It is axiomatic that all populations would be, at some point, limited by their food supply; I therefore assume that this stable equilibrium must be present in all defoliating insect systems.

Another System

Before examining the remaining processes, I must present evidence from another defoliating insect system, European pine sawfly, *Neodiprion sertifer*, for the sake of completeness (Wallace and Griffiths, in prep.). I have not included this system in my previous analyses because the European pine sawfly/red pine model has a forest submodel which is not amenable for the analytical approach I have taken in this thesis.

Figure 56, an isorecruitment curve for the defoliator from the European pine sawfly model, shows that an upper stable equilibrium caused by the effects of intra-specific competition exists at a high insect density and a stable equilibrium caused by small mammal predation exists at an intermediate insect density. This density is very similar to the intermediate stable equilibrium in the jack pine sawfly/jack pine model. There is no low density stable equilibrium.
Figure 56: A representative isorecruitment curve from the European pine sawfly/red pine model. The upper stable surface is set by intra-specific competition; the lower stable surface is set by small mammal predation.
Avian Predation

Avian predation, if it occurs, creates a stable defoliator equilibrium at a low density, and the presence of avian predation can be predicted by knowing the effectiveness of defoliator predator defense mechanisms.

The lower stable equilibrium in the equilibrium structures of the two budworm and of jack pine sawfly is created by avian predation, and avian predation always creates a stable surface at a very low defoliator density in the models. This stable surface does not exist in the equilibrium structure for European pine sawfly. European pine sawfly is the only system of the four in which predation by birds is minimal. European pine sawfly larvae are colonial and are capable of actively repelling avian predators (Prop 1960). Eastern spruce budworm (Morris 1963) and eastern black-headed budworm (Miller 1966) are solitary as larvae, while jack pine sawfly, although colonial, is not able to effectively defend itself against avian predation (McLeod 1977a). The presence or absence of avian predation on the defoliator therefore determines presence or absence of a stable defoliator equilibrium at a very low defoliator density.

The above suggests that bird predation, if it is present, will create a low density stable equilibrium for the defoliator. This depends critically on two definitions. First, the stable equilibrium created by avian predation must always be at a very low density ("low" in this case is defined relative to what outbreak densities normally are).
Second, the form of the predator functional response must be Type III (Holling 1959), so that the mortality rate due to them must increase over some increasing range of defoliator densities as the predator switches to the defoliators from some other food source.

To test whether both these conditions are valid, I gathered defoliator mortality data from avian predation from as many sources as possible with defoliator densities measured in the same units as each other. Unfortunately, such data have been collected for very few cases. The data sets I could find are presented in Figure 57, along with mortality curves fitted using non-linear parameter estimation (UBC 1975). The mortality curve is derived from the generalized functional response presented in Mace et al. (1978).

The peak mortalities for the three cases occur from 0.5 to 5 larvae/m² of ground. This is a wide range of defoliator density, but all peak predation rates occur at densities which are low relative to outbreak densities for these defoliators. Furthermore, in 2 out of 3 data sets, there is a range of defoliator densities over which mortality from avian predation increases. This limited evidence does indicate that avian predators of defoliators have their greatest effect at very low defoliator densities and they may create a potential stable equilibrium at those densities.

Small Mammal Predation

Small mammal predation, if it occurs, creates a defoliator equilibrium at an intermediate defoliator
density and the presence of small mammal predation can be predicted by knowing the location of defoliator pupation.

The intermediate stable equilibrium for jack pine sawfly and European pine sawfly is caused by small mammal predation. An intermediate stable surface does not exist for either budworm. Both budworm species pupate at the point of their final feeding, in the tree crowns (Morris 1963, Miller 1966); they are therefore relatively invulnerable to predation by small mammals which inhabit the forest floor. Both sawflies pupate on the ground below the forest canopy (McLeod 1966, Wallace and Griffiths, in prep); they are therefore vulnerable to predation by the small mammals which inhabit the forest floor. Location of pupation, then, determines presence or absence of predation by small mammals which, in turn, determines presence or absence of a stable surface for the defoliator at intermediate densities.

As with avian predation, my claim about small mammal predation depends on two conditions. First, the peak of small mammal predation must be at similar densities for all defoliators. Second, the form of the functional response by small mammal predators must be Type III (Holling 1959) so that the mortality rate due to them will increase over an increasing range of defoliator density.

I gathered suitable small mammal predation data sets from as many defoliating insect systems as possible. Like the avian predation data sets, there are very few cases in which the proper data for this analysis have been collected.
I used the published mortality curves in cases where I could not get the raw data.

Both these conditions are met, however, for the three examples I could find (Figure 58). This limited evidence shows that small mammal predation, if it occurs, can create a potential stable surface at an intermediate defoliator density.

Summary

Of the four processes described above, intra-specific competition always occurs and avian and small mammal predation are either present or absent. Therefore, there are 2, or 4 possible defoliator equilibrium structures (Figure 59).

6.7.2 The Other Variables

The foliage, parasitoid, disease, and forest variables have the same equilibrium structure in all defoliating insect systems.

In all 3 models, foliage, parasitoid, and forest have a single stable equilibrium, the position of which increases with decreasing defoliator, increasing defoliator, and increasing foliage densities, respectively. Therefore, there is no need to determine what factors will give rise to alternate equilibrium structures for these variables.

The equilibrium structure of the disease models developed by Anderson (1979) and Anderson and May (1980) have a single stable surface, much like that in Figure 3. Therefore, I will assume that the disease variable has a
Figure 58: Small mammal predation data from various defoliating insect systems. ● - European spruce sawfly data from Neilson and Morris (1964). JPS - fitted curve to jack pine sawfly data from McLeod (unpublished data). EPS - fitted curve to European pine sawfly data from Holling (1959).
single stable equilibrium, and that the position of this equilibrium is set by the pathogenicity of the disease, and the length of the infective stage.

6.7 Summary

I have derived an integrative theory for the structure and behavior of defoliating insect systems. The key elements of the theory are:

1. the structure and behavior of an defoliating insect system can be explained with five dynamic variables -- the defoliator, the foliage, the forest, the parasitoid, and the disease -- and the effects of weather acting on the defoliator;

2. there are 4 classes of defoliating insect system behavior;

3. the behavior that an defoliating insect system will exhibit is determined by the magnitude of weather effects on defoliator survival and recruitment, the parasitoid numerical response to changing defoliator densities, the disease numerical response to changing defoliator densities, and the vulnerability of the forest to defoliation;

4. there are 4 structures the defoliator can exhibit, and one each for the parasitoid, the foliage, the forest, and the disease; and
5. defoliating insect system structure and behavior can be predicted with a particular, well-defined set of information (Table VIII).
Table VIII: Information necessary to predict the structure and behavior of insect/forest systems.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Structure</th>
<th>Behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td>Defoliator</td>
<td>1. Effectiveness of larval predator defense mechanisms 2. Location of pupation</td>
<td>1. Comparative development rates in different geographical locations</td>
</tr>
<tr>
<td>Disease</td>
<td>1. Pathogenicity 2. Length of infective stage 3. Defoliator recruitment rate</td>
<td></td>
</tr>
<tr>
<td>Foliage</td>
<td>1. Time to full foliage for different defoliation levels</td>
<td></td>
</tr>
<tr>
<td>Forest</td>
<td>1. Tree mortality for different defoliation levels</td>
<td></td>
</tr>
</tbody>
</table>
7.0 TESTING THE THEORY

7.1 Introduction

The integrative theory for the structure and behavior of defoliating insect systems developed in Chapter 6 cannot be proved correct. It can only be disproven. However, if the theory stands up in the face of invalidation attempts, one's confidence should increase that the theory provides a useful and predictive method for analyzing the dynamics of defoliating insect systems.

The most convincing tests of ecological hypotheses are field experiments. Too many models are constructed with little or no empirical basis or cannot be tested or parameterized with direct experimentation. The theory I have developed, however, can be tested empirically. The most convincing field experiments are those which would test whether an experimental perturbation to a defoliating insect system did indeed have the consequences for equilibrium structure and system behavior that the theory predicted. Because of the time scales of the system components involved, these experiments would not be trivial. Years, perhaps even decades, would be needed before the theory could be tested. However, as actual field experiments provide the best mechanism for evaluating the theory, I will outline and describe specific field experiments which would test the theory.

In the absence of field experiments to test the theory,
existing data collected on defoliating insect system can be used for simple invalidation tests. These data can be examined for particular behaviors or structures predicted by the theory. This approach presents some problems and some opportunities.

First, there is still the problem of time scales. Such long term data, for Class 4 systems for example, would have to span approximately 100 generations for them to be remotely useful. Even then, only one defoliator outbreak may be represented. These types of data sets simply do not exist. Second, most long term data collected on defoliating insect systems consist almost entirely of defoliator population estimates. The other 3 system components which the theory uses have never been censused with the regularity that defoliator populations have, let alone with the regularity needed to test the theory.

However, these long term defoliator population data could be used to test specific hypotheses relating to defoliator equilibrium structure and behavior derived from the theory. A part of my invalidation will use these long term population data to test parts of the integrative theory related to the defoliator.

Also, in spite of the absence of long term data on all 4 components of defoliating insect systems used in the theory, 2 sources contain extremely good qualitative accounts of the temporal behavior of all components of
defoliating insect systems: the annual reports of the Canadian Forest Insect and Disease Survey, beginning in 1939 and continuing to the present, and review articles of major defoliating insect system studies (e.g., eastern spruce budworm, Morris 1963, European spruce sawfly, Neilson and Morris 1964). These studies and reports will be used to test how well the qualitative patterns of behavior predicted by the theory compare with the accounts of defoliating insect system behavior reported in these sources.

7.2 Field Experiments

The core of the theory is that it is possible to predict equilibrium structure and behavior of defoliating insect systems from simple sets of information. There are 2 field experiments which need to be undertaken to test this notion. The first relates to the idea that a simple information set can be used to predict equilibrium structure, the second relates to the idea that a simple information set can be used to predict temporal behavior.

7.2.1 A Field Experiment For Testing Equilibrium Structure

The theory predicts that defoliators which have poor or no larval defense mechanisms and pupate on the ground will have 3 stable equilibria, one at a very low density set by avian predators, one at an intermediate density set by small mammal predators, and one at a very high insect density set by limitation in the food supply. Beginning with a defoliator at very low population levels, removal of the 2 relevant
sources of predation should cause the defoliator population to increase. Furthermore, once the defoliator population had increased, adding the sources of predation back in to the system should not cause the defoliator population to decline.

Therefore, this experiment should take the following form (Figure 60). A system should be chosen for which the theory predicts the defoliator has 3 equilibria; that is, the defoliator must have no larval predator defense mechanisms and must pupate in the ground. Defoliator populations should be at very low levels (less than 10 eggs/m²). Defoliator populations in the stands in which the experiment are to be done should be censused for a number of insect generations before the perturbations are done to make sure that experimental behaviors are a cause of the perturbation and not standard behaviors for the system in those stands. The experiment should occur in stands of mature host forest to remove effects of forest immaturity on system dynamics (Figures 15, 31, 47).

The experiment should be in stands where outbreaks have occurred previously so the experimenter can be sure the effects of heavy larval mortality from weather conditions can be removed. Finally, each treatment should be on a sufficiently large spatial scale to remove effects of defoliator dispersal (Clark 1979) or predator aggregation (Blais and Parks 1964, Mattson et al. 1968).
Figure 60: Experiment to test for defoliator equilibrium structure. Birds are removed from Stand B and birds and small mammals are removed from Stand C. Stand A is a control.
One stand (A) should be a control, with no predator removal. The first treatment (B) should consist of removing avian predators. The second treatment (C) should consist of removing both avian and small mammal predators. The theory predicts that defoliator populations in A should remain at very low levels, populations in B should increase to intermediate levels (100 to 200 eggs/m²), and populations in C should increase to very high levels (about 1000 eggs/m²). These levels should be reached 2 to 4 years after the initiation of predator removal.

When these shifts in population have been demonstrated, about 5 years after initial predator removal, predators should be allowed back into the treatment areas. Defoliator populations should not decline to control level populations, but should remain at their respective increased levels. This final step is necessary to control for the possibility that the initial increases in population were simply due to removal of mortality sources. If the theory is not invalid, allowing the predator guilds to recolonize the treatment stands should not cause defoliator populations to decline. The total time period of this test would be about 15 years, from initial censusing of defoliator populations.

Similar experiments have been attempted in the gypsy moth/oak system (Campbell and Sloan 1977). Both birds and small mammals were removed from parts of red oak stands and defoliator populations censused. However, the predator guilds were allowed back in to the stands too soon after
removal and the role of these predators in defining the
defoliator equilibrium structure was not conclusively demon-
strated.

7.2.2 A Field Experiment For Testing System Behavior

The integrative theory states that the difference
between a Class 3 or 4 system and a Class 2 system is simply
the time scale of the parasitoid. Class 3 and 4 systems
have a slow parasitoid, while Class 2 systems have a fast
parasitoid, relative to the defoliator. It should therefore
be possible to shift the behavior of a Class 2 system to
either a Class 3 or 4 by "slowing down" the parasitoid.
"Slowing down" the parasitoid is a relatively easy task. It
occurs often, for example, in agricultural pest systems when
excessive pesticide applications are used and remove most of
a particular pest's natural enemy guild (van den Bosch
1979).

The experiment should take the following form (Figure
61). A system should be chosen in which the historical evi-
dence shows the behavior to be Class 2. Again, experimental
stands should be sufficiently large to remove potentially
confounding effects of defoliator dispersal and predator
aggregation.

The treatment (B) in the second stand should consist of
reducing parasitoid progeny survival for a number of years.
This could be achieved by release of sterile parasitoid
males (in non-parthenogenic species) or trapping parasitoid
Figure 61: Experiment to test whether the integrative theory can predict class of behavior. Parasitoid recruitment is reduced in Stand A between time I and II. The theory states that system behavior should shift to a Class 3 or Class 4 from a Class 2 system.
males with pheromones (again in non-parthenogenic parasitoid species). The hypothesis predicts that the system should immediately acquire the characteristics of either a Class 3 or 4 system. The theory predicts that it is possible to predict the class of behavior by knowing probability of tree mortality under low foliage conditions.

Once the new class of behavior has been conclusively demonstrated, the treatment causing the reduction in parasitoid progeny survival should be terminated. The integrative theory predicts that the behavior of the system should return to that of a Class 2. This experiment would take approximately 20 years to complete. This time frame allows for 1 outbreak cycle for each behavior class.

Fortunately, the classic examples of biological control provide evidence that differences in the time scale of the parasitoid can create dramatic shifts from one class of behavior to another in defoliating insect systems (e.g., Neilson and Morris 1964, Turnock 1972, Section 7.4).

7.3 Equilibrium Structure In Long Term Population Data

If multiple equilibria exist in defoliator populations, then perhaps they can be revealed in long term population data. There is no certainty that they can because the defoliator population may have never moved into the region of one or more of the equilibria during the time the data were collected. The theory would be supported, though, if analyses showed or suggested insect populations contained
multiple equilibria.

I know of no statistical methods to test for multiple equilibria in population data. Therefore, I will identify patterns which appear in long term data for a defoliator which is known to be multiply stable and see if these patterns appear in other defoliator population data. I will choose gypsy moth as the defoliator on which to identify these patterns. Many gypsy moth scientists agree that the defoliator is multiply stable and that this multiple stability is reflected in the historical population data (Doane and McManus 1977, Campbell and Sloan 1978).

Gypsy Moth Population Data Analysis

The integrative theory predicts that gypsy moth should have three equilibria, as it pupates on the ground and has no larval predator defense mechanisms (Bess 1961). The long term population data for gypsy moth (Appendix I) from 1911 to 1932 show a consistent pattern characterized by an initial period (1911-1921) of high population levels followed by a rapid decline to a lower population state (1922-1932). The initial period was marked by high defoliation rates and reduced tree growth and forest vigor and the latter period was marked by very little defoliation and higher gypsy moth parasitism rates (Doane and McManus 1977). Vertebrate predation rates were not measured for this period. In addition, more recent data from a site in which gypsy moth is present but has never caused defoliation (Figure 62) show
Figure 62: Gypsy moth population dataset from a non-outbreak location in New York. Data from Campbell and Sloan (1978).
extremely low population levels. Campbell (1976) showed that populations in this area were subject to extremely high vertebrate predation.

I performed a cluster analysis on the four datasets from 1911-1932 coupled with the data from Figure 62 using the SYSTAT statistical package (SYSTAT 1985). Cluster analysis is an analytical procedure for combining samples into like groups. There are many different types of cluster analysis procedures, and different clustering algorithms will produce different sample groupings. In this case, I used an algorithm which clustered according to average Euclidean distance.

The results show that clustering into 2 population groups from 3 gives the largest increase in the distance measure between population groups. This means that 3 population groups is the most appropriate level of clustering. The data points in each of the 3 groups selected by the cluster analysis represent the 1911-1921, 1922-1932, and the data in Figure 62. Also, the increase in the distance measure when the populations are clustered from 3 to 2 groups accounts for over 50% of the final distance measure. The greater the proportion of the final distance measure accounted for by a clustering, the larger the differences between the groups being clustered. Finally, the integrative theory predicts that the defoliator should have 3 stable equilibria. The fact that the cluster analysis reveals 3 population groups to be the most appropriate
clustering is encouraging.

But, it is important to emphasize what exactly the results of using this statistical technique mean. The results show very clearly that historical gypsy moth population data can be aggregated into a small set of groups and that the differences between these groups are large. The results also show that the number of clusters predicted by the integrative theory are also reflected in the datasets. This does not mean, however, that the processes hypothesized in the integrative theory to create multiple equilibria were operating at each of these population levels. The rates of vertebrate predation from 1922 to 1932 were not measured. Furthermore, the results do not provide conclusive proof that the groups or clusters are distinct and separate population equilibria. Gypsy moth may have only a single equilibrium which shifts in response to one of the factors described in Chapter 2, such a foliage quality. Only the field experiments described above can provide conclusive evidence. On the other hand, the results do show that the gypsy moth exists in distinct population states. They also increase degree of belief in the concept of multiple stability in gypsy moth populations and that the integrative theory does properly predict gypsy moth equilibrium structure.

The Analysis Procedure

Given the above results for gypsy moth, a cluster
analysis of the population datasets presented in Appendix I should demonstrate that the number of stable equilibria predicted by the integrative theory should be the same as the number of clusters, or population groupings, observed in the datasets.

I performed a cluster analysis for each population dataset contained in Appendix I, selected the most significant population grouping as measured by the % of the final distance measure made by the next clustering, and compared the number of groupings with the number of equilibria predicted by the integrative theory based on predator defense and location of pupation.

Results

Table IX shows that the majority of the population datasets contain 2 or 3 population groupings. 26% of the datasets had significant clustering (Table X), using a significance criterion of 50% of final distance measure. 40% of the datasets for which 2 clusters were predicted and 5% of the datasets (i.e., only one population dataset) for which 3 were predicted met this 50% criterion. 57% of the datasets for which the integrative theory predicts 2 stable equilibria had 2 population clusters (irrespective of level of significance), while 53% of the datasets for which the integrative theory predicts 3 stable equilibria had 3 population clusters, again irrespective of level of significance (Table XI).
Table IX: Number of population groups predicted by the cluster analysis.

<table>
<thead>
<tr>
<th>Number Of Population Groups</th>
<th>Number Of Datasets</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>51</td>
</tr>
<tr>
<td>3</td>
<td>19</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>6</td>
<td>2</td>
</tr>
</tbody>
</table>
Table X: Significance of cluster analysis results for datasets in which 2 or 3 population groups were selected. Significance is defined by the % of the total distance measure with the succeeding cluster (cluster to 1 in the case of 2 population groups or to 2 in the case of 3 population groups). I assume 50% as being significant.

<table>
<thead>
<tr>
<th>% Of Total Distance Measure With Next Cluster</th>
<th>Number Of Population Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
</tr>
<tr>
<td>0- 10</td>
<td>0</td>
</tr>
<tr>
<td>10- 20</td>
<td>4</td>
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<tr>
<td>20- 30</td>
<td>8</td>
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<td>30- 40</td>
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<td>50- 60</td>
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<td>60- 70</td>
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<tr>
<td>70- 80</td>
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</tr>
<tr>
<td>80- 90</td>
<td>4</td>
</tr>
<tr>
<td>90-100</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>51</td>
</tr>
</tbody>
</table>
Table XI: Comparison of number of population groups selected by cluster analysis with number predicted by integrative theory. Table entries are number of datasets.

<table>
<thead>
<tr>
<th>Number Of Groups Predicted By Theory</th>
<th>2</th>
<th>3</th>
<th>&gt; 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>34</td>
<td>14</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
<td>12</td>
<td>4</td>
<td>2</td>
</tr>
</tbody>
</table>
The results on a defoliator basis (Table XII) show that there are defoliators, particularly gypsy moth and saddle-back looper, for which the clustering analysis results match the predictions of the integrative theory, in that the majority of their datasets have highly significant numbers of the predicted number of clusters. In another group of defoliators, including Douglas-fir tussock moth, western blackheaded budworm, western spruce budworm, western hemlock looper, European pine sawfly, a majority of datasets contain the same number of population groups selected by the cluster analysis as the number predicted by the integrative theory, although fewer of these are significant, using the 50% of final distance measure criterion. The results of a third group, including green striped forest looper, western false hemlock looper, larch sawfly, pine looper, jack pine sawfly, and European spruce sawfly do not match the predictions at all well.

The results show that the integrative theory has moderate success at predicting the number of equilibria in defoliator populations using this technique.

7.4 Test Of System Behavior

The integrative theory holds that 4 classes of defoliating insect system exist, and that the periodicities of various events, such as defoliator outbreaks, are different in the different behavior classes. If the theory is valid, then differences in defoliator population outbreak frequen-
Table XII: Cluster analysis results for each defoliator. Entries are number of datasets. Bold entries indicate the number of population groups predicted by the integrative theory. Numbers in brackets refer to total number of datasets.

<table>
<thead>
<tr>
<th>Defoliator</th>
<th>Significant</th>
<th># Population Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>Saddleback</td>
<td>Y</td>
<td>4</td>
</tr>
<tr>
<td>Looper (7)</td>
<td>N</td>
<td>2</td>
</tr>
<tr>
<td>Green striped</td>
<td>Y</td>
<td>2</td>
</tr>
<tr>
<td>Forest Looper (12)</td>
<td>N</td>
<td>4</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>Y</td>
<td>2</td>
</tr>
<tr>
<td>Tussock Moth (6)</td>
<td>N</td>
<td>3</td>
</tr>
<tr>
<td>Western False</td>
<td>Y</td>
<td>2</td>
</tr>
<tr>
<td>Hemlock Looper (12)</td>
<td>N</td>
<td>3</td>
</tr>
<tr>
<td>Western Black-headed Budworm (7)</td>
<td>Y</td>
<td>1</td>
</tr>
<tr>
<td>Western Spruce Budworm (15)</td>
<td>N</td>
<td>3</td>
</tr>
<tr>
<td>Larch Sawfly (5)</td>
<td>Y</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>2</td>
</tr>
<tr>
<td>Gypsy Moth (4)</td>
<td>Y</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
</tr>
<tr>
<td>Pine Looper (2)</td>
<td>Y</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>2</td>
</tr>
<tr>
<td>Jack Pine Sawfly (1)</td>
<td>Y</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
</tr>
<tr>
<td>European Pine Sawfly (1)</td>
<td>Y</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>0</td>
</tr>
<tr>
<td>European Spruce Sawfly (1)</td>
<td>Y</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>1</td>
</tr>
</tbody>
</table>
cies should be apparent in defoliator population data. Unfortunately, none of the population datasets span a sufficient period of time to allow for any Class 4 behavior to appear. Furthermore, I do not expect any outbreaks from Class 1 systems. Therefore, this analysis focused on Class 2 and 3 systems, and the hypothesis I tested is that outbreak frequencies from Class 2 and Class 3 systems are different. The procedure I used on the datasets in Appendix I is:

1. predict, using the integrative theory, the behavior class for each defoliating insect system (Class 2 or 3);

2. using spectral analysis (Fox and McGuire 1975) determine the periodicity of defoliator outbreaks, defined by the periodicity with the highest spectral density (only those datasets in which the spectrum was statistically shown not to be flat, i.e., the spectral analysis did not distinguish a periodicity as dominant) for each dataset; and

3. test, using a t-test, whether the periodicities from each behavior class are different.

A total of 91 population sets with significant spectral densities were selected (there are more population sets, 91, than datasets, 80, because some of the datasets, such as those for gypsy moth, could be divided into two or more
periods). Frequency distributions of the periodicities (Figure 63) show that there is a separation in defoliator outbreak frequencies between Class 2 and Class 3 systems. 61 of the 91 datasets were predicted to be Type 2 systems while 17 of the 91 datasets were predicted to be Type 3 systems. The test of the hypothesis that the 2 classes do have different periodicities gave a t value of 2.95. This is significant (p < .01) and the 2 sets of periodicities are statistically different. The result of this test provides more evidence that the simple information set defined in the integrative theory can be used to predict the proper class of behavior of defoliating insect systems.

A feature of the outbreak periodicities of the Class 3 systems worth noting is the high number of datasets which have a very low periodicity (2-3 years). These samples are from the gypsy moth/red oak system. The gypsy moth feeds on red oak, a host tree which retains only one year of foliage at any time. The majority of the other samples from Class 3 systems are from the western spruce budworm/Douglas fir system. This budworm feeds on Douglas fir, a host tree which retains 8 years of foliage (Silver 1960). The foliage variable has very different time scales in these 2 systems, and these different time scales appear are reflected in the dominant outbreak periodicities.

7.5 Tests Using Information Set

I tested the predictive power of the integrative theory
Figure 63: Frequency distributions of dominant periodicities found in long term defoliator population data.

a. From those systems predicted to be Class 2.
b. From those systems predicted to be Class 3.
by using the minimum information set to predict the class of behavior the system should exhibit and comparing predicted behavior with documented behavior from annual reports of the Canadian Forest Insect and Disease Survey and synthesis articles of defoliating insect systems.

I had difficulty in finding evidence of weather-induced mortality effects on defoliator populations in specific geographical locations. If a system exhibited 2 types of behavior, I could only rarely point to weather effects as being the major difference. This is not surprising, as most forest entomological work has been done on systems which have been managed for outbreak containment for some time. These are invariably systems in which the defoliator has caused outbreaks and some damage to the forest; I therefore concentrated on those systems which were not Class 1. I also found that there are very few systems for which the minimum information set needed to predict behavior exists. Of all the systems described in Table III, only six of them had all the required information set. The information on the parasitoid or disease variable was usually lacking.

The results of this test (Table XIII) show that the integrative theory described in Chapter 6, modified with the changes described above for foliage recovery times, has good predictive power for all six defoliating insect systems. It predicts natural system dynamics, shifts in behavior caused by successful introduction of biological control agents (larch sawfly, 1921-1940; gypsy moth in U.S.A after 1921),
Table XIII: Comparison of predicted with documented behavior class.
Unless mentioned, behavior is for system in Canada.
See Table XIV for references for this information.

<table>
<thead>
<tr>
<th>Defoliator</th>
<th>Host Tree</th>
<th>Type Of Numerical Response Indicated By Parasite Or Disease Information</th>
<th>Tree Mortality With High Defoliation</th>
<th>Predicted Behavior Class</th>
<th>Documented Behavior Class</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western Spruce Budworm</td>
<td>Douglas-fir</td>
<td>parasite, slow</td>
<td>low</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>European Spruce Sawfly</td>
<td>White spruce</td>
<td>no parasite or disease</td>
<td>low</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>European Spruce Sawfly</td>
<td>White spruce</td>
<td>parasite, rapid</td>
<td>low</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Larch Sawfly before 1912</td>
<td>tamarack</td>
<td>no parasite or disease</td>
<td>low</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Larch Sawfly 1912-1940</td>
<td>tamarack</td>
<td>parasite, rapid</td>
<td>low</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Larch Sawfly after 1940</td>
<td>tamarack</td>
<td>no, encapsulation of host</td>
<td>low</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>
Table XIII: Continued

<table>
<thead>
<tr>
<th>Defoliator</th>
<th>Host Tree</th>
<th>Type Of Numerical Response Indicated By Parasite Or Disease Information</th>
<th>Tree Mortality With High Defoliation</th>
<th>Predicted Behavior Class</th>
<th>Documented Behavior Class</th>
</tr>
</thead>
<tbody>
<tr>
<td>Douglas-fir tussock moth</td>
<td>Douglas-fir</td>
<td>disease, rapid</td>
<td>high</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Winter moth before 1958</td>
<td>red oak</td>
<td>no parasite or disease</td>
<td>low</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Gypsy moth in U.S.A before 1922</td>
<td>white oak</td>
<td>no parasite or disease</td>
<td>low</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Gypsy moth in U.S.A after 1922</td>
<td>white oak</td>
<td>disease, rapid</td>
<td>low</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Gypsy moth in Europe</td>
<td>white oak</td>
<td>disease, rapid</td>
<td>low</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>
Table XIV: Literature sources for the information contained in Table XIII.

<table>
<thead>
<tr>
<th>Defoliator</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western Spruce Budworm</td>
<td>Dodge (1961), Silver (1960), Canada (1939-1982), Johnson and Denton (1975)</td>
</tr>
<tr>
<td>European Spruce Sawfly</td>
<td>Reeks and Barter (1951), Neilson and Morris (1964), Webber (1932), Reeks (1953)</td>
</tr>
<tr>
<td>Larch Sawfly</td>
<td>Craighead (1940), Turnock (1972), Graham (1952), Muldrew (1953)</td>
</tr>
<tr>
<td>Douglas-fir Tussock Moth</td>
<td>Thompson (1979), Silver (1960), Sugden (1957), Shepherd and Otvos (1986)</td>
</tr>
<tr>
<td>Winter Moth</td>
<td>Embree (1965), Embree (1966), Embree (1967)</td>
</tr>
</tbody>
</table>
failures of those biological control agents (larch sawfly after 1940), and system behavior in widely different geographical areas (gypsy moth in U.S.A and in Europe). The exception is with Douglas-fir tussock moth. All the biological information suggests it should be a Class 2 system, but the level of tree mortality in some stands suggests that its impact on the host forest is more like that exhibited in a Class 4 system (Shepherd and Otvos 1986).

These results, plus the results of the time series analysis, suggest that the theory is, in general, a good framework for understanding and explaining the behavior of defoliating insect systems. Obviously, more testing needs to be done to clearly identify where the framework does and does not work.
8.0 CONCLUSIONS AND RESEARCH IMPLICATIONS

8.1 Conclusions

The major conclusions of this thesis, in terms of the objectives set out in Section 1.2 are:

1. the structure and behavior of a defoliating insect system can be explained with five dynamic variables -- the defoliator, the foliage, the forest, the parasitoid, and the disease -- and the effects of weather acting on the defoliator;

2. there are 4 classes of defoliating insect system behavior;

3. the behavior that a defoliating insect system will exhibit is determined by the magnitude of weather effects on defoliator survival and recruitment, the parasitoid numerical response to changing defoliator densities, the numerical response of the disease to changing defoliator densities, and the vulnerability of the forest to defoliation;

4. there are 4 equilibrium structures the defoliator can exhibit, and one each for the parasitoid, the foliage, the forest, and the disease; and

5. defoliating insect system structure and behavior can be predicted with a particular, well-defined set of information.
I must emphasize at this point, however, that the concepts developed in this thesis remain largely untested, and must therefore still be viewed as simply an approach by which the structure and behavior of defoliating systems can perhaps be understood. The lack of data for testing the components of the theory, so clearly demonstrated in Chapter 7, preclude the concepts from being well tested. This means that it is difficult to currently clearly define those cases for where the concepts and theory do apply and those cases in which they do not. Only experiments similar to those described in Chapter 7, and the collection of the minimum information set outlined in Chapter 6 will be able to definitively test the concepts. In addition, there are at least two major areas which remain unresolved: hypotheses for defoliating insect system behavior which are not a part of this theory; and the spatial dynamics of these systems. These are discussed below.

8.2 Relationship To Previous Theories

The integrative theory developed in this thesis does not supplant any previous theories of defoliating insect system structure and behavior. No new classes of explanation, such as predation or food quality, are proposed. However, it is unusual in the sense that it does not explain the structure and behavior of simply one particular system on the basis of factors or processes specific to that system in the way that previous analyses do (Wellington et al. 1975, McLeod 1977a, Brookes et al. 1979, Clark and Holling
Rather, it is a general framework with unusual properties when viewed in the light of previous theories.

First, certain previous theories have a well defined role in this integrative theory. The role of predation is defined by a guild of tree crown-searching natural enemies and a guild of ground-searching natural enemies; these guilds create temporary stable defoliator population states at densities well below outbreak. The role of weather is to remove upper stable equilibria by reducing defoliator generation survival. Parasitism and disease infection have the role of potentially collapsing defoliator outbreaks.

Second, the integrative theory is sufficiently general that it is able to define specific conditions under which particular structures and behaviors will occur. It therefore can be used to predict the structure and behavior of a wide variety of defoliating insect systems.

8.3 Factors Not Included

The integrative theory does not utilize all previous theories. In particular, the theories involving foliage quality, individual differences in defoliators, and defoliator dispersal are not used in the integrative theory.

8.3.1 Dispersal

The process of defoliator dispersal is part of the larger question of defoliating insect system spatial dynam-
ics. I suspect that a comprehensive examination of the spatial dynamics of defoliating insect systems can only be addressed by an approach similar to the one taken in this thesis. There is certainly evidence that an integrative theory for the spatial dynamics of defoliating insect systems can be developed. For example, there appear to be a few qualitatively different spatial behaviors:

1. "spreading wave" - historical eastern spruce budworm (Clark 1979), eastern black-headed budworm (Miller 1966), western spruce budworm (Shepherd et al. 1979),

2. "synchronous localized" - gypsy moth (Doane and McManus 1981), Douglas-fir tussock moth (Brookes et al. 1979); and

3. "asynchronous localized" - jack pine budworm (Canada 1939 to 1982), managed eastern spruce budworm (Clark 1979).

Such an integrative theory would outline the minimum set of processes necessary to capture all the potential spatial behaviors and the conditions under which each behavior is likely to occur. I suspect that the following components may be important in developing this integrative theory:

1. the primary life stage in which dispersal occurs (larva as in Douglas-fir tussock moth or gypsy
moth, or adult as in jack pine budworm or eastern spruce budworm);

2. the primary method of dispersal (physical flight as in all sawflies, or wind-assisted dispersal as in jack pine budworm or eastern spruce budworm);

3. qualitatively different "exodus" and "settling" functions (Clark 1979); and

4. the spatial pattern of the "habitat" (discontinuous as in the British Columbia mountain ranges, or homogeneous as in the tamarack forests of the North American midwest or plantation forests).

I point out here, however, that Clark (1979) found that the behavior of the eastern spruce budworm system was explainable by local dynamics, modified to account for exodus and settling of dispersing budworm. This must be considered as a caution to anyone undertaking such a task.

8.3.2 Individual Differences

Individual differences have no role in the integrative theory of defoliating insect systems, yet they have been shown to be critically important in the dynamics of a number of forest insect pests (Chapter 2). It is probable that the role of individual differences is important in spatial dynamics and it is there that the role of individual differences would best be placed. For example, Clark (1979) used it extensively in developing alternate budworm dispersal
functions.

8.3.3 Foliage Quality

As with individual differences, foliage quality is not a part of this integrative theory. I suspect that the only appropriate method of testing whether foliage quality can determine defoliating insect/system behavior would be to attempt to initiate outbreaks by altering foliage quality.

8.4 Implications For Insect/Forest System Research

The results of this thesis demonstrate clearly that it is not necessary to assume, as has been assumed in the past, that each defoliating insect system is unique and different from all others. At the very least, the integrative theory implies that, with less effort than has historically been thought necessary, the equilibrium structure and the behavior of these systems can be induced. Also, the information that is needed to accomplish this is clear. Once this information is known, very simple models of the system of concern can be developed using specific biological and behavioral data. These models can then used to define research questions more specific to the particular system.

The results of this thesis also have particular implications for the emphasis which needs to be placed on particular types of research in forest entomology.

8.4.1 The Defoliator

Defoliator research need not be as extensive as it has
been traditionally. Typically, the majority of the budget in forest pest research programs is allocated to studying the defoliator (e.g., Morris 1963, Brookes et al. 1979). This is not necessary. The results of this thesis suggest that extensive life table studies and detailed predator studies which census the types of predators and their effects at different population levels -- research which is invariably undertaken at high cost -- need not be done. What is needed to induce the equilibrium structure of the defoliator is the location of its various life history stages and the efficacy of its predator defense mechanisms.

8.4.2 The Parasitoid And Disease Complexes

The results of this thesis imply that a rigorous, quantitative understanding of the dynamics of the parasitoid and disease complexes of defoliators is critical to understanding defoliating insect systems. Unfortunately, the research into these natural enemy guilds is usually descriptive. In terms of these two natural enemy complexes, the state of understanding is as poor as the state of understanding of defoliator population dynamics before the major defoliator research programs of the last 25 years.

Research into parasitoid and disease guilds should be 'population dynamic' in nature. For parasitoids, this means life table analyses, behavioral studies estimating attack rates and the level of super-parasitism and discrimination between parasitized and non-parasitized hosts. For disease
complexes, future research should integrate the current understanding of the dynamics of the pathogen within the host with a good understanding of the dynamics while the pathogen is outside the host.

8.4.3 The Foliage

As with parasitoid and disease complexes, foliage research tends to be minimal and restricted to predicting foliage biomass as a function of various tree attributes. Foliage research should concentrate on estimating foliage recovery times after defoliation. This information is crucial to determining whether the system of interest is a Class 3 system, operating on a defoliator:foliage cycle, or a Class 4 system, operating on a defoliator:parasitoid or disease cycle.

8.4.4 The Forest

The results of this thesis imply that the equilibrium structure of the forest can be induced by knowing the probability of tree mortality when heavy defoliation occurs during the time of year when the defoliator does the majority of its feeding. This in turn implies that the equilibrium structure is largely a function of characteristics of the trees themselves and is somewhat independent of the defoliator of concern. That is, if this information is known for a particular tree species and a particular defoliator, it can be used for another system in which a different defoliator feeds at the same time of the year. Therefore, forest
research need only be undertaken if the tree species has never experienced heavy defoliation during the time of year when the defoliator of concern feeds.

If such a condition occurs, research should be undertaken to find out the probability of tree mortality under these conditions. The artificial defoliation experiments of Craighead (1940) are certainly examples of the type of research which might be undertaken. Another approach would be to let the defoliator perform the experiment. This would mean sacrificing some forest stands to defoliator outbreaks and monitoring the mortality response of those stands.
9.0 LITERATURE CITED


Holling, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population
regulation.


McLeod, J.M. in prep. The Swaine jack pine sawfly life system model.


(Lepidoptera: Tortricidae) in British Columbia. Can. Ent. 116: 375-381.


van den Bosch, I. 1979. The Pesticide Conspiracy.


8 pp.


A.I APPENDIX I - TIME SERIES AND SPECTRAL DENSITIES FOR DEFOLIATOR POPULATIONS

The following figures are the defoliator population datasets used in the analyses throughout the thesis. In addition, the spectral densities are given for each dataset; these were derived from the datasets by using the MIDAS statistical package (Fox and Guire 1976). The spectral densities are used in Table III, Chapter 2, the review of insect/forest system behavior and in Chapter 7, testing for classes of insect/forest system behavior. The population data are used in Chapter 7, in the testing for multiple stable equilibria in defoliator populations. Table II lists the data sources used in the compilation of these datasets.

Each dataset has two graphs. The first a graph of the population over time. The populations were transformed to their common logarithm before plotting and all are scaled from -3 (=.001) to 4 (=10,000). A vertical bar for a given at the top of the graph signifies a year in which the population estimate was 0. The absence of a vertical bar or a population point means no data were gathered. Most of these graphs represent a single region or plot. A number of time series are presented on the same graph in those systems where the data are relatively short term but from a series of plots (e.g., jack pine sawfly).

Below each graph is the normalized spectral density for the dominant dataset in each time series. A representative spectral density is presented for those datasets where the
data are relatively short term but from a series of plots.
Western False Hemlock Looper
Green-Striped Forest Looper
Green-Striped Forest Looper
Douglas-fir Tussock Moth
Douglas-fir Tussock Moth
Western Hemlock Looper
Larch Sawfly
Western Spruce Budworm
Western Blackheaded Budworm
Gypsy Moth
Saddlebacked Looper
A.II APPENDIX II - ANALYSIS OF PARASITOID ISORECRUITMENT CURVES

The parasitoid submodel in the three insect/forest models can be collapsed to the following general equation:

\[ P_{t+1} = N(1 - \left( \frac{(aP_tN)/(1+bN))/(kN) \right)^{-k} ce, \text{ where} \]

- \( P_{t+1} \) the parasitoid density in the succeeding generation;
- \( P_t \) the parasitoid density in the current generation;
- \( N \) host (defoliator) density;
- \( a, b \) parameters of the parasitoid functional response to host density;
- \( k \) the dispersion coefficient of the negative binomial equation;
- \( c \) the survival of attacked hosts during the time before parasitoid emergence;
- \( e \) the survival of the parasitoid from the time of emergence from the host to the time of attack in the next generation.
The components of this model are:

1. a Type 2 functional response to host density (Hol­ling, 1959);

2. a competition equation (the negative binomial) which accounts for the effects of contagion in the distribution of attacks among the prey. The negative binomial zero term gives the proportion of the host population which is not attacked by parasitoids. The assumption is that parasitoids cannot or do not discriminate between non-parasitized and previously parasitized hosts, and that only one parasitoid can emerge from an attacked host; irrespective of the number of parasitoid eggs originally laid in that host;

3. a survival of hosts from the time of attack by the parasitoid to the time of parasitoid emergence from the host (parameter $c$); and

4. a parasitoid progeny survival rate (parameter $e$) from the time of parasitoid emergence from the host to the time those progeny re-attack the in the succeeding generation.

Parameters $c$ and $e$ are simply scalars to the parasitoid recruitment function. They do not determine the shape of the isorecruitment curve and will therefore be left out of
the remaining analysis.

We can look at the effect that the parasitoid functional response has on the shape of the isorecruitment curve by removing the competition equation from the model. Ignoring parameters \( c \) and \( e \), the model therefore simplifies to:

\[
\frac{P_{t+1}}{P_t} = \frac{aN}{1+bN} \quad (A.2)
\]

I want to find all values of \( N \) for which \( \frac{P_{t+1}}{P_t} = 1 \); that is, all host density values from which there is no change in the parasitoid population from one generation to the next. These densities form the parasitoid isorecruitment curve. Rearranging equation A.2, one gets:

\[
\frac{aN}{1+bN} = 1 \quad (A.3)
\]
Rearranging terms gives:

\[ aN = 1 + bN \]
\[ bN - aN = 1 \]
\[ N(a-b) = 1 \]
\[ N = \frac{1}{a - b} \]

Therefore, without the competition equation, the density of hosts which create equilibrium parasitoid densities is \( \frac{1}{b-a} \). The parasitoid isorecruitment curve under these conditions is a vertical line at \( N = \frac{1}{b-a} \) and unlike the isorecruitment curves derived from the three insect/forest models. The isorecruitment curve for equation A.2 (without the competition equation) is what the isorecruitment curve would be in the insect models if there were no effects of egg distribution, and that all parasitoid eggs laid would emerge from the host.

The conclusion is that it is the competition equation which causes the parasitoid isorecruitment curves to bend over at high parasitoid densities. The reason for this is that, with increasing number of parasitoid attacks (which occurs with increases in parasitoid densities) the number of successful attacks, defined by the number of parasitoid progeny which emerge from the hosts, relative the number of attacks made by the parasitoids, decreases. It decreases
because of the assumption that only one parasitoid progeny can emerge from a host, irrespective of the number of eggs laid in that host.