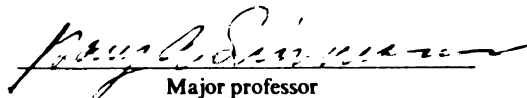


This is to certify that the
dissertation entitled
Studies Related to the Concept of Pest - Crop System Design:
1) Adult Parasitoid Activity and Its Relation
to Biocontrol and 2) Forest Harvesting
and the Spruce Budworm
presented by
Jan Peter Nyrop

has been accepted towards fulfillment
of the requirements for
Ph.D. Entomology
_____ degree in _____


Major professor

Date 10-20-82



RETURNING MATERIALS:

Place in book drop to
remove this checkout from
your record. FINES will
be charged if book is
returned after the date
stamped below.

--	--	--

STUDIES RELATED TO THE CONCEPT OF PEST - CROP SYSTEM DESIGN:

1) ADULT PARASITOID ACTIVITY AND ITS RELATION
TO BIOCONTROL AND 2) FOREST HARVESTING
AND THE SPRUCE BUDWORM

by

Jan Peter Nyrop

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Entomology

1982

ABSTRACT

**STUDIES RELATED TO THE CONCEPT OF PEST-CROP SYSTEM DESIGN:
1) ADULT PARASITOID ACTIVITY AND ITS RELATION TO BIOCONTROL AND
2) FOREST HARVESTING AND THE SPRUCE BUDWORM**

By

Jan Peter Nyrop

Damage to crops from pest organisms can be controlled two ways. First, the structure of the crop production system can be accepted as is and the pest organisms controlled in some fashion. Second, the structure of the crop production system can be manipulated so that pest damage is minimized. In this thesis the latter concept is explored in two studies.

In the first project, the temporal and spatial dynamics of an adult parasitoid (Glypta fumiferanae Vierick) were assessed and related to the theory of parasitoid-host dynamics. This was done because adult parasitoids and factors influencing them may be objects of control for system management.

Field data on adult parasitoid activity was used to construct a model relating activity to weather. Historical data were then examined to determine if weather induced changes in parasitoid activity were reflected in changes in parasitism. I concluded cool, wet weather inhibited parasitoid host searching and attack.

Observations of G. fumiferanae attacking hosts suggested the parasitoid does not forage optimally. An experiment was conducted to determine whether light and/or temperature influenced parasitoid foraging behavior. The experiment indicated this was the case.

The empirical studies were related to parasitoid-host theory which was then revised. This revision consisted of redefining the attributes of a successful biocontrol agent to be one which has a high searching efficiency but need not aggregate in areas of high host density.

In the second project, the use of forest harvesting was explored as a way to change the structure of the spruce budworm/forest system and thereby improve system control. A theoretical basis for the strategy was developed, an economic analysis was made and the strategy was field tested. Results from the field test did not substantiate the theory on the effect of partial harvesting on budworm dynamics. As a result, the test was inconclusive.

to Jessica Erin

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to Gary Simmons for serving as my advisor, for providing intellectual stimulation, encouragement, and for being a friend. To my committee, Drs. Dean Haynes, Lal Tummala, Stuart Gage and Gary Fowler I extend my appreciation for their guidance and patience during my graduate training. Special thanks go to Dr. James Bath who, as Department Chairman, has provided an atmosphere conducive to professionalism and at the same time enjoyable to work in.

A large group of people assisted in collecting data for this thesis. I thank them all. I especially wish to thank Marcia McKeague for her involvement in the early stages of the forest harvesting study and James Pieronek for his help in constructing an environmental chamber.

Finally, I wish to thank Jerryvonne Nyrop for her help in data collection and manuscript preparation.

TABLE OF CONTENTS

Introduction	1
Adult Parasitoid Activity and Its Relation to Biocontrol	3
Introduction	4
Methods and results	6
Field studies of adult parasitoid activity	6
Sampling methods	6
Analysis	14
Laboratory studies of host searching behavior	26
Experimental design	26
Analysis	30
Historical data on parasitoid-host interactions	33
Description of data	33
Analysis	35
Discussion	40
Relation to other studies	40
Parasitoid-host models and biological control	42
A revised parasitoid-host model	46
Attributes of a successful biocontrol agent	54
Conclusions	55
Forest Harvesting and the Spruce Budworm	58
Introduction	58
Strategies for controlling budworm damage	59
A theoretical basis for partial forest harvesting	61
Previous studies	61
Mathematical analysis	66
Implementation and assessment of partial cut strategy	78
Description of study areas	78
Feasibility analysis	80
Economic considerations	85
Biological response of the system	91
Dispersal loss of budworm	92
Predation and parasitism	96
Conclusions	102
Conclusions	104
Appendices	106
Appendix 1: Distributed delays as models of insect life stages ..	106
Appendix 2: Temperature controller for environmental chamber ..	108
Appendix 3: Mathematical methods for analysis of parasitoid- host models	109

Appendix 4: Computer program listings	111
Appendix 5: Analysis of the economics of partial cuts	122
Appendix 6: Form sent to loggers to determine cost and returns .	124
Appendix 7: Bird census data	126
Appendix 8: Additional malaise trap data and analysis	130
Appendix 9: Spruce budworm population data	135
Appendix 10: Voucher specimen sheet	143
Literature Cited	145

LIST OF TABLES

TABLE	PAGE
1. Models used to predict the temporal distribution of malaise trap catch of female <u>Glypta fumiferanae</u>	20
2. Distribution of attacks by <u>Glypta fumiferanae</u> on spruce budworm larvae in balsam fir trees (n = 16). The exterior of the tree denotes the first 18 inches of the canopy.	28
3. Total time and time spent in attack and non-attack behavior by <u>Glypta fumiferanae</u> in different environmental regimes.	31
4. Julian dates for the degree day interval 428 - 584 (base 8.89 °C) and precipitation during this period in the years 1950 to 1957 at the Green River field station, New Brunswick.	36
5. Equilibrium points and eigenvalues of a parasitoid host model linearized about these points.	50
6. Comparison of species composition of live trees and tree condition parameters for spruce budworm host trees by treatment in stand 1.	81
7. Comparison of species composition of live trees and tree condition parameters for spruce budworm host trees by treatment in stand 2.	82
8. Comparison of species composition of live trees and tree condition parameters for spruce budworm host trees by treatment in stand 3.	83
9. Costs and revenues incurred by logger in harvesting stand 3. .	89
10. Dates and degree days (base 5.56 °C) for five sampling periods during which spruce budworm densities were determined in three stands. Peak 3rd instar occurs at c. 167 dd, peak 6th instar at c. 416 DD and initial emergence of male moths at c. 472 DD.	91

TABLE

PAGE

11.	Density per m ² balsam fir foliage of various life stages of the spruce budworm in 1981 and percentage mortality due to parasitism and unknown causes in stand 1.	93
12.	Density per m ² balsam fir foliage of various life stages of the spruce budworm in 1981 and percentage mortality due to parasitism and unknown causes in stand 2.	94
13.	Density per m ² balsam fir foliage of various life stages of the spruce budworm in 1981 and percentage mortality due to parasitism and unknown causes in stand 3.	95
14.	Defoliation of balsam fir by spruce budworm in three stands in which part of the stand was partially harvested and the other part served as a control.	101
15.	Malaise trap catch of female <u>Glypta fumiferanae</u> from two plots and weather data in 1982. One trap was located in 24 jack pine in each plot. Twelve traps were in the upper crown and 12 in the lower crown.	133

LIST OF FIGURES

FIGURE		PAGE
1.	Location of study plots in Michigan's Upper Peninsula	7
2.	Details of a malaise trap designed for placement in tree crowns	8
3.	Catch of female <u>Glypta fumiferanae</u> from 14 malaise traps located in balsam fir trees in stand 1 during 1980	10
4.	Catch of male and female adult <u>Glypta fumiferanae</u> from 13 malaise traps located in balsam fir trees in stands 2 and 3 during 1981	11
5.	Bi-hourly trap catch of female <u>Glypta fumiferanae</u> from 13 malaise traps located in balsam fir trees in stand 2 and the temporal distribution of temperature and rainfall	13
6.	General structure of the model used to analyze the temporal distribution of malaise trap catches of <u>Glypta fumiferanae</u> . <u>W</u> is a vector of weather variables and <u>a</u> is a proportionality parameter	16
7.	Observed combined emergence of adult male and female <u>Glypta fumiferanae</u> in stand 2 and predicted emergence of female <u>G. fumiferanae</u> as a function of degree days base 8.89° C	19
8.	Predicted and actual malaise trap catch of adult female <u>Glypta fumiferanae</u> in stand 2 and the theoretical, relative temporal distribution of adult females. Malaise traps were located singly in 13 balsam fir trees	22
9.	Predicted and actual malaise trap catch of adult female <u>Glypta fumiferanae</u> in stand 3 and the theoretical, relative temporal distribution of adult females. Malaise traps were located singly in 13 balsam fir trees	24
10.	Temporal relationships between the density per 10 m ² foliage of second instar (L ₂) spruce budworm, the density of adult female <u>Glypta fumiferanae</u> and the percentage of third and fourth instar (L ₃ -L ₄) budworm parasitized by <u>G. fumiferanae</u> in three plots at the Green River field station, New Brunswick	38
11.	Parasitism of spruce budworm larvae by <u>Glypta fumiferanae</u> as a function of the ratio of hosts to parasitoids and rainfall during the period of adult parasitoid activity	39

FIGURE	PAGE
12. Net recruitment for an insect population preyed upon by a constant density of predators which exhibit a sigmoidal functional response	48
13. Influence of parasitoid aggregation with respect to host density on the stability region of a parasitoid host model ..	52
14. Influence of parasitoid host searching efficiency on the stability region of a parasitoid host model	53
15. The relationship between the rate of increase of spruce budworm populations (solid line) and different levels of predation and parasitism (dashed lines)	63
16. The influence of different levels of dispersal loss and predation on the rate of change of spruce budworm numbers ...	68
17. The influence of spruce budworm defoliation on the survival of host trees	74
18. Influence of spruce budworm on the physiological condition of host trees	77
19. Layout of cut and control areas in stands 1, 2 and 3	79
20. Relationship between the mean annual increment and the current increment in timber volume growth	84
21. The density per m^2 foliage of various life stages of the spruce budworm in the cut and control areas of stand 3	98
22. The density per m^2 foliage of various life stages of the spruce budworm in the cut and control areas of stand 2	99
23. The density per m^2 foliage of various life stages of the spruce budworm in the cut and control areas of stand 1	100
24. Circuit diagram for temperature controller of an environmental chamber. The portion to the right of the dashed line is replicated for each group of heating elements	108
25. Proportion of total malaise trap catch of female <u>Glypta fumiferanae</u> for 7 time intervals within a day. The sample period was 6 days (7-19 to 7-24). One trap was located in 48 jack pine trees. Twenty four traps were located in the upper crown and 24 in the lower crown	132

26. Malaise trap catch of female Glypta fumiferanae from two plots in relation to degree days base 8.9 °C in 1982. One trap was located in each of 24 jack pine in each plot. Twelve traps were in the upper crown and 12 in the lower crown 134

INTRODUCTION

An inherent aspect of most crop production systems is the necessity to take into account the influence of crop damaging organisms. Two different, though not mutually exclusive, approaches can be adopted. First, the structure of the crop production system can be accepted as is and pests can be controlled in some fashion. The structure of a system refers to the physical and institutional properties of the system and policies which, once implemented, usually cannot be changed. The structure of crop production systems involves a number of diverse factors such as crop variety, crop spacing and mixing, the genetic makeup of plants and pests, crop markets, and society's expectations of crop consumption. With the first approach, chemical toxicants are most often used to either drive a pest species as close to extinction as possible or preserve the integrity of the host plant.

Increasing social and economic costs of chemical pesticides, reports of their deleterious effects, and the significant rate at which they fail to prevent crop damage make it apparent that the application of pesticides can no longer be an exclusive pest control policy. With the advent of integrated pest management, inputs of pesticides have been reduced in some crop production systems. For the most part, however, this has been accomplished by improving the decision making process of when and how much of a pesticide to apply as opposed to reducing reliance on pesticides as a control tool.

The second approach, which might also be considered the second phase of pest management, is to consider pests and factors which influence pest dynamics as an integral part of the crop production system and design a system structure so that the effects of pest organisms are minimized (Haynes et al. 1980). This will be

a formidable task. As in the design of an electronic amplifier, it will necessitate the wedding of theory (often couched in terms of mathematics) and empirical observations. However, unlike the amplifier, pest crop systems are "badly defined systems" (Beck 1981, Young 1978). With such systems, a priori theory usually cannot predict the nature of the system and design cannot come about from theory alone. Furthermore, planned experiments with these systems are often difficult and may at times be impossible to implement. Even in situ data of the "normal operation" of the system may be difficult to acquire.

Although the obstacles to this approach seem insurmountable, it must be pursued vigorously if pest management is to become what the name implies. In this thesis, I present the results of two projects which were motivated by the concept of design. In both, an effort is made to make use of theory and empirical data in an effort to propagate the concept of system design and to develop principles appropriate to each area of study. In the first project, the temporal and spatial dynamics of an adult parasitoid of the spruce budworm were investigated. This was done to develop methods for sampling this important life stage of parasitoids and to develop concepts appropriate to design-mediated biological control. In the second project, the use of forest harvesting was explored as a way to change the structure of the spruce budworm/spruce fir forest system and thereby improve system control. No pretense existed of actually being able to meet this entire objective. However, the project was pursued in hopes of establishing a basis for further study in this area.

**Adult Parasitoid Activity and
Its Relation to Biocontrol**

Introduction

Actions taken to achieve or improve control of crop damaging insects using parasitoids fall into three endeavors: importation of exotic parasitoids, augmentation of established exotic or endemic parasitoids, or management of existing parasitic insects. Management entails any action taken to improve the effectiveness of a parasitoid as a control agent. When applicable, management should be the first action taken. Furthermore, when management can be implemented, it will likely be more cost effective than importation or augmentation.

Knowledge of factors which influence the life system of a parasitic insect and information on how these factors may be manipulated are prerequisites for successful parasitoid management. One of the most important aspects of the life system of parasitic insects is host searching since the maximum number of progeny that can be produced by a generation of parasitoids is determined by their host searching efficiency. Therefore, the adult female parasitoid and factors which influence the number and distribution of hosts attacked by the female may be important objects of control in any management effort.

Numerous theoretical investigations have examined the relationships between the host distribution, parasitoid host searching behavior and resultant dynamics of parasitoid-host systems. Based on these studies, the characteristics of successful biological control agents have been advanced (Beddington et al. 1978). In all of these studies the only factors influencing parasitoid host searching are the density and distribution of hosts. However, factors other than the host influence parasitoid searching behavior. Few field studies have been undertaken to elucidate these factors. This is in part because such studies should

focus on the temporal and spatial dynamics of the adult parasitoid. These organisms are small, highly mobile and most often few in number and as such are difficult to sample. Even fewer studies have sought to juxtapose empirical observations of the adult parasitoid and the theory of parasitoid-host systems. Investigations of this type are necessary though if the chasm between empirical observations and parasitoid-host theory is to be bridged and, concurrently, our ability to manage parasitoids broadened.

In this paper we present the results of an investigation of the spatial and temporal dynamics of adults of the parasitoid Glypta fumiferanae Vierick. G. fumiferanae is a common, specific, univoltine parasitoid that attacks first and second instar spruce budworm (Choristoneura fumiferana (Clemens)). It overwinters in the budworm larvae and emerges from either fifth or sixth instar hosts. It then spins a pupal case in the tree and emerges as an adult at approximately the time when budworm eggs are eclosing. Details of the biology of G. fumiferanae are provided by Brown 1946, Wilkes et al. 1948, Dowden et al. 1948, and Miller 1960.

The paper consists of three sections. First, information on the temporal and spatial dynamics of adult G. fumiferanae is presented. Data was obtained through field studies of the activity patterns of the parasitoid and through a laboratory investigation of host searching behavior in a gradient of abiotic environments. Second, the relationship between the temporal dynamics of the adult parasitoid and its searching efficiency is examined using historical data of the interaction between G. fumiferanae and its host. Finally, the general implications of our findings are assayed. This is done by relating our observations to established parasitoid-host theory and to extensions of this theory which we have developed.

Methods and Results

Field Studies: Data was collected on the temporal and spatial activity patterns of adult G. fumiferanae during 1980 and 1981 in northern Michigan. One forest stand was sampled in 1980, and two stands were sampled in 1981 (fig. 1). The study area used in 1980 was not used in 1981 because it was cut for timber.

Based on previous sampling of adult parasitoids (Julliet 1963, Price 1971, Reardon et al. 1977, Ticehurst and Reardon 1977, Simmons unpubl. data), malaise traps were selected as the principal tool for measuring the activity patterns of adult G. fumiferanae. Malaise traps are ideally suited for this task because they are passive traps and snare actively flying insects. The traps were designed and constructed for placement in tree crowns and on the forest floor; this way trap catch could be easily inspected. Details of trap design and construction are given in figure 2.

During early July 1980, 14 of these traps were placed in the mid to upper crowns of 14 balsam fir (Abies balsamea (L.) (Miller)), and 14 were placed on the forest floor in stand 1 (fig. 1). Traps were placed on the forest floor because it was hypothesized that G. fumiferanae might use this habitat when foraging for food. The forest floor provides a habitat for many plants which produce nectar and pollen. These plant products have been cited as food for adult parasitoids by many authors (Chermokova 1960; Lewis 1960, 1961a, 1961b, 1963, 1967; Shahjahan 1974; Simmons et al. 1975; Syme 1966, 1975; Thorpe and Caulde 1938).

Stand 1 consisted of ca. 60% mature balsam fir. Trees in which traps were placed were selected on the basis of ease of access for trap placement and good crown condition. Traps were positioned in the trees so that one open side of the

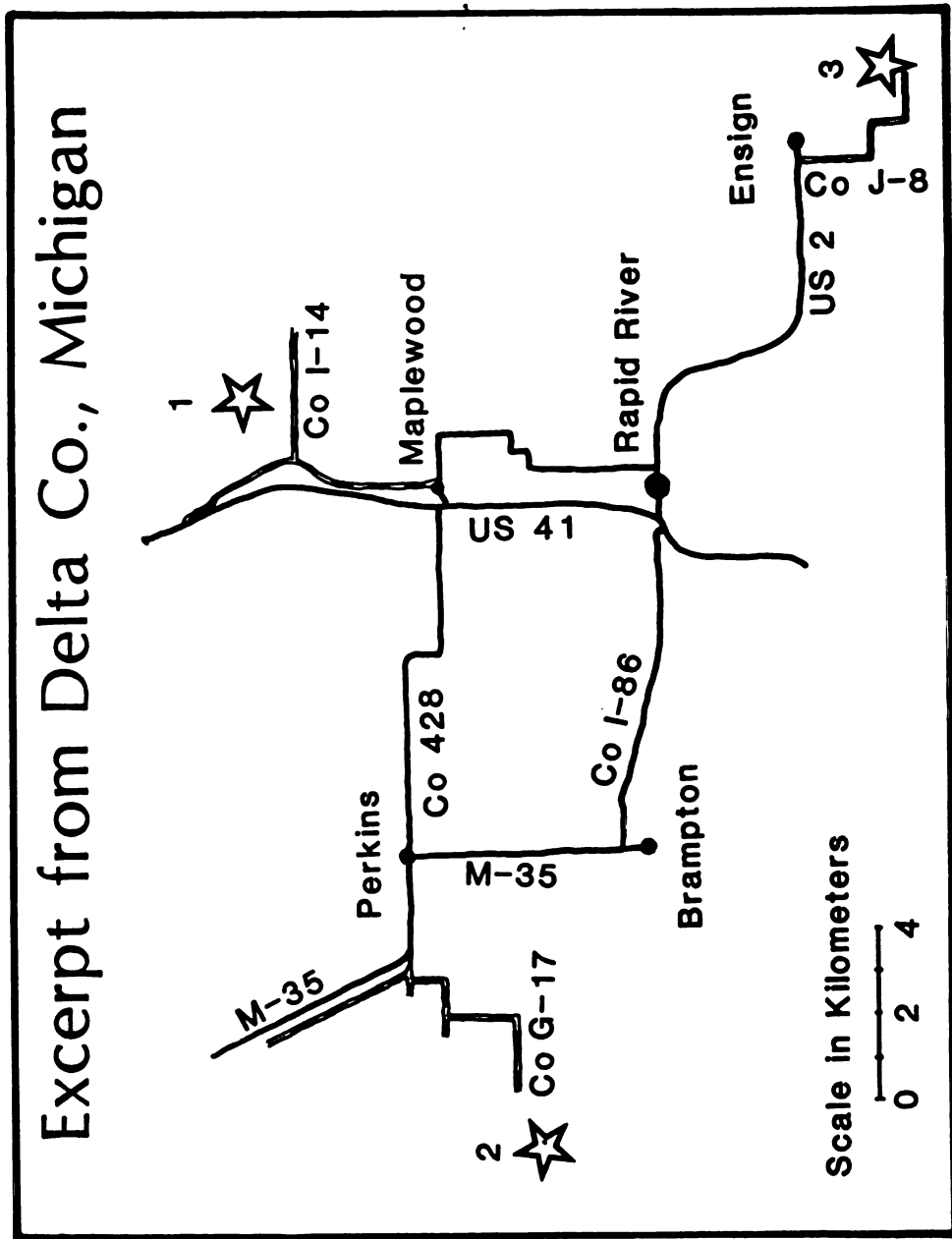


Figure 1. Location of study plots in Michigan's Upper Peninsula.

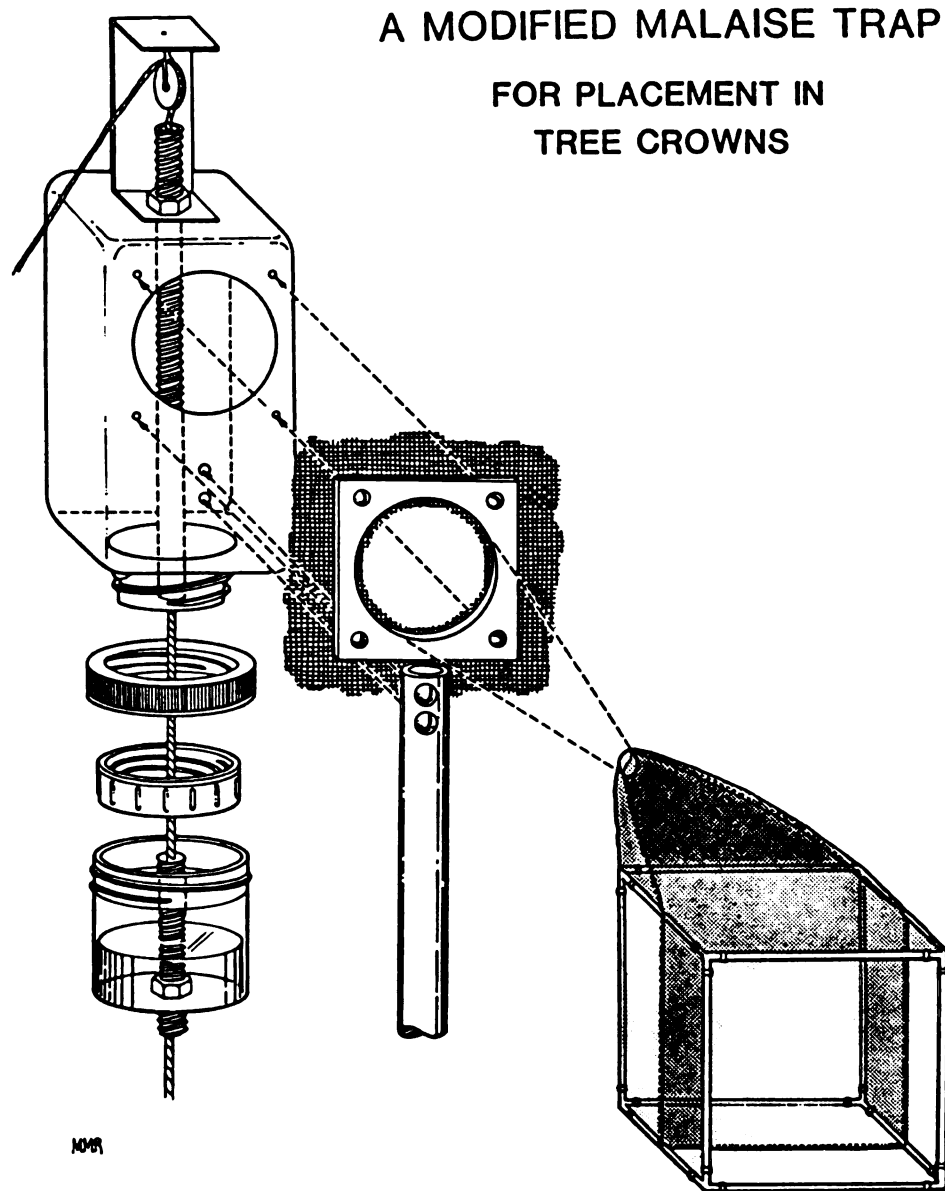


Figure 2. Details of a malaise trap designed for placement in tree crowns. Trap volume is 1 m^3 . The frame is constructed of PVC pipe and the screening of Saran 20 mesh screening. The intermediate and final collection jars and the face plate are plastic. The final collection jar is affixed to a nylon cord which passes through a threaded pipe which is in turn attached to the intermediate collection jar. Trap catch is inspected by lowering the final collection jar.

trap was tangent to the tree crown. G. fumiferanae pupal density per m² balsam fir foliage was 7.61 (s=10.02, n=48). Traps were emptied each morning between 10 July and 10 August. In total, 39 females were trapped in the trees (fig. 3), and none were caught on the forest floor.

We felt that the low trap catch in 1980 may have been due to the orientation of the traps in the tree crowns. Therefore, in 1981 the traps were oriented so that the open sides were perpendicular to the crown. Thirteen traps were located in balsam fir and 13 on the forest floor in stands 2 and 3 (fig. 1). Stand 2 was 100% mature balsam fir and stand 3 ca. 50% mature balsam fir. The density of G. fumiferanae pupae per m² balsam fir in stands 2 and 3 was 10.45 (s=11.28, n=40) and 9.87 (s=9.03, n=40). Traps were emptied each morning between 2 July and 15 August. During the peak flight of females, traps in stand 2 were emptied bi-hourly from 800 to 2200 hours for 3 days. In total, 125 males and 294 females were trapped in trees in stand 2, and 72 males and 182 females were trapped in trees in stand 3 (fig. 4). Clearly, the orientation of the traps in the trees during 1981 was superior and indeed necessary for capturing significant numbers of G. fumiferanae. No parasitoids were trapped on the ground.

The flight activity as measured by trap catch of both males and females in stands 2 and 3 during 1981 are remarkably similar (fig. 4). Hence, we hypothesized that weather was a major determinant of flight activity. This hypothesis was supported by the bi-hourly trap catch data for females in stand 2 (fig. 5). This data indicated that parasitoid flight activity was strongly depressed by rain. On 17 July rain began ca. 1500 hours resulting in a decline in female activity as measured by trap catch. Activity also followed the daily temperature profile.

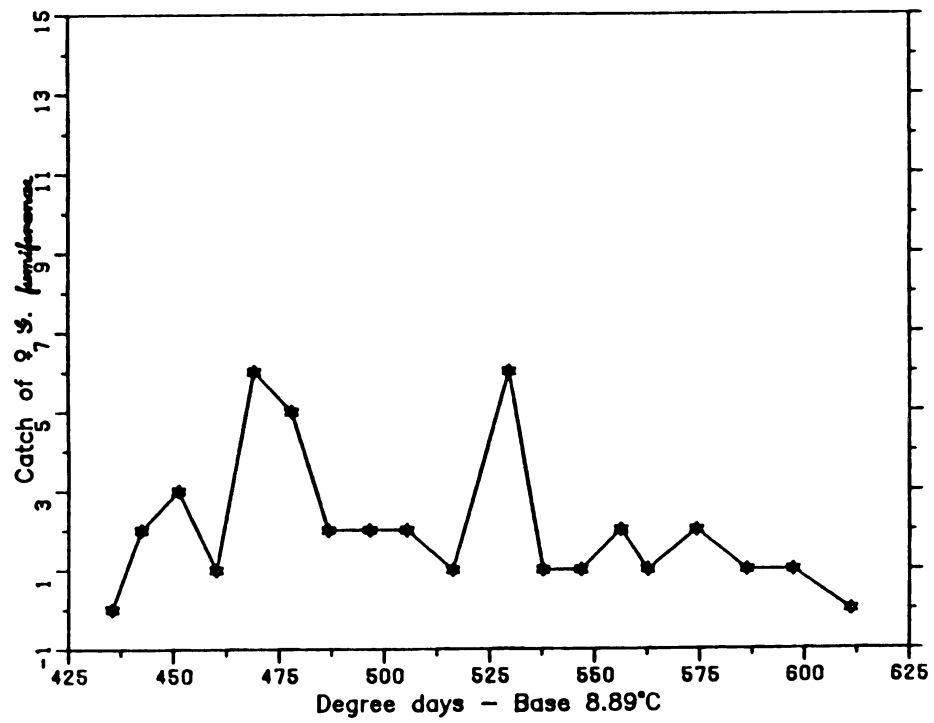
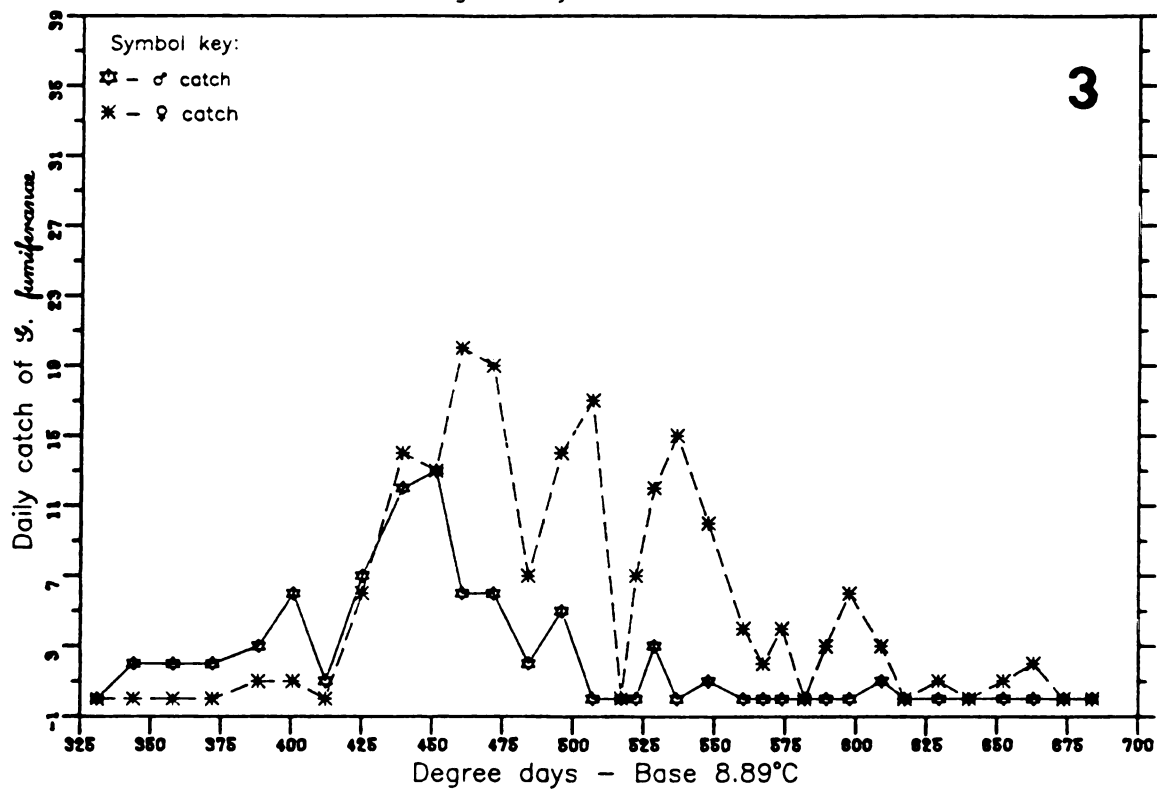
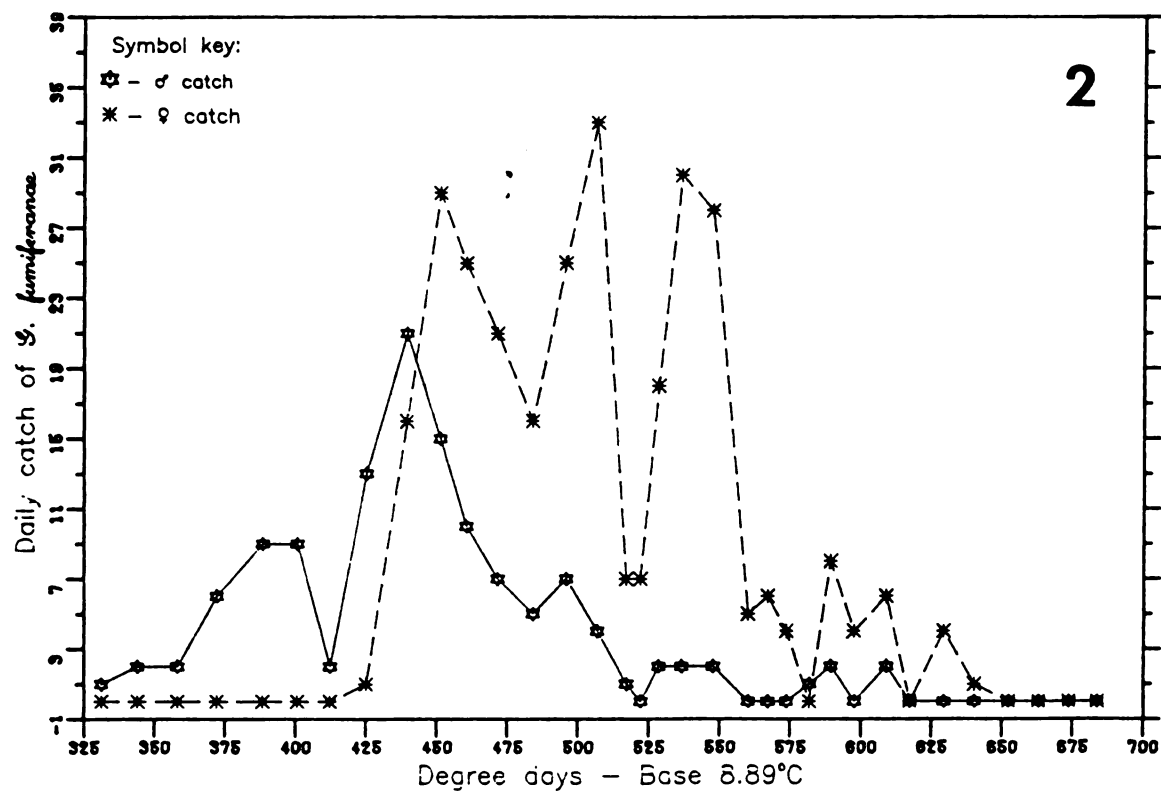


Figure 3. Catch of female *Glypta fumiferanae* from 14 malaise traps located in balsam fir trees in stand 1 during 1980.

Figure 4. Catch of male and female adult Glypta fumiferanae from 13 malaise traps located in balsam fir trees in stands 2 and 3 during 1981.



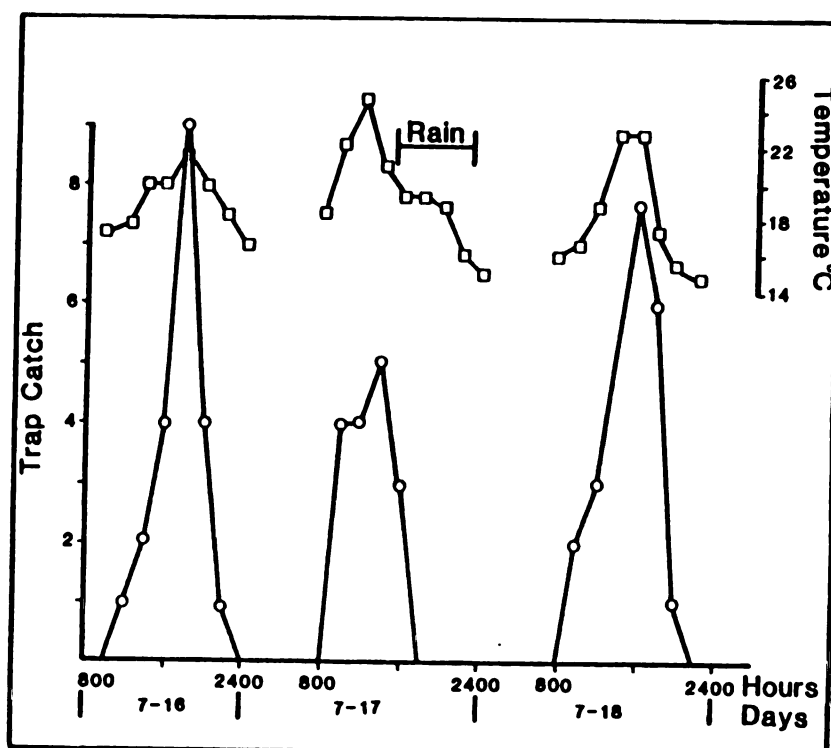


Figure 5. Bi-hourly trap catch of female *Glypta fumiferanae* from 13 malaise traps located in balsam fir trees in stand 2 and the temporal distribution of temperature and rainfall.

In order to examine the influence of rainfall and other possible weather factors more extensively, a model was constructed so that the relationship between weather and the time series of trap catches could be examined. A modelling approach was adopted because conventional statistical methods could not be used in analyzing this relationship. This is because trap catch in the absence of any other influencing factors would be proportional to the density of adult parasitoids. This density was unknown. However, with the assumptions outlined below, an index of this density could be derived from the trap catch data.

In the model, predicted trap catch (TC) of G. fumiferanae was expressed as a function of adult density (Ad) and adult activity (Aa). In addition, the activity of the adults was related to a set of weather variables (W). These relationships are concisely written as:

$$TC = f(Ad, Aa) \quad (1)$$

$$Aa = f(W)$$

The time-specific adult density, $Ad(t)$, is not known. However, it is a function of the emergence, dispersal and death processes operating until time t . With the assumptions that dispersal into and out of an area balance and that either a constant or no external mortality operates on the adult population, $Ad(t)$ is a function of the emergence rate and physiological time interval between emergence and death. With these assumptions, our modelling methodology can be outlined as follows: 1) specify a function for the change in adult density through physiological time, 2) specify a function relating trap catch to adult density and weather, 3) parameterize a model based on these functions through the use of a nonlinear optimization algorithm, and 4) evaluate model fit by

comparing predicted trap catch to the data with which the model was parameterized and to an independent data set. Physiological time was approximated with degree days (DD) (base 8.89°C), and the model was parameterized with the data collected from stand 2.

The general structure of the model is given in figure 6. $Ad(t)$ is the integral of the difference between the emergence and adult mortality rates. Each of these rates was modelled as a distributed delay. These delays can be used to model aggregate processes which are made up of entities in which each entity has an output related to its input via a pure time delay. In this case the emergence of a parasitoid is related to some initial time point and its death is related to its emergence via two physiological time delays (PTD).

For a population of parasitoids, a PTD is a random variable. It can be shown that the distributed delay is based on the probability density function (pdf) of a PTD (appendix 1). If $f(t)$ is the pdf of the physiological time delay between emergence and death, and $p(t)$ and $m(t)$ are the emergence and mortality rates, then:

$$m(t) = \int_0^t p(v)f(t-v)dv \quad \text{where } t = \text{physiological time.}$$

The adult density is given by:

$$Ad(t) = \int_0^t p(v)-m(v)dv$$

The parameters for the emergence rate were estimated from data on the cumulative emergence of G. fumiferanae collected in stand 2. Those for mortality were estimated jointly with other model parameters from the trap catch data. The gamma density function with an integer shape parameter (k) was used for $f(t)$. The shape parameter was determined by initially selecting a value based on the shape of the distribution of $p(t)$ and $Ad(t)$ and then adjusting it

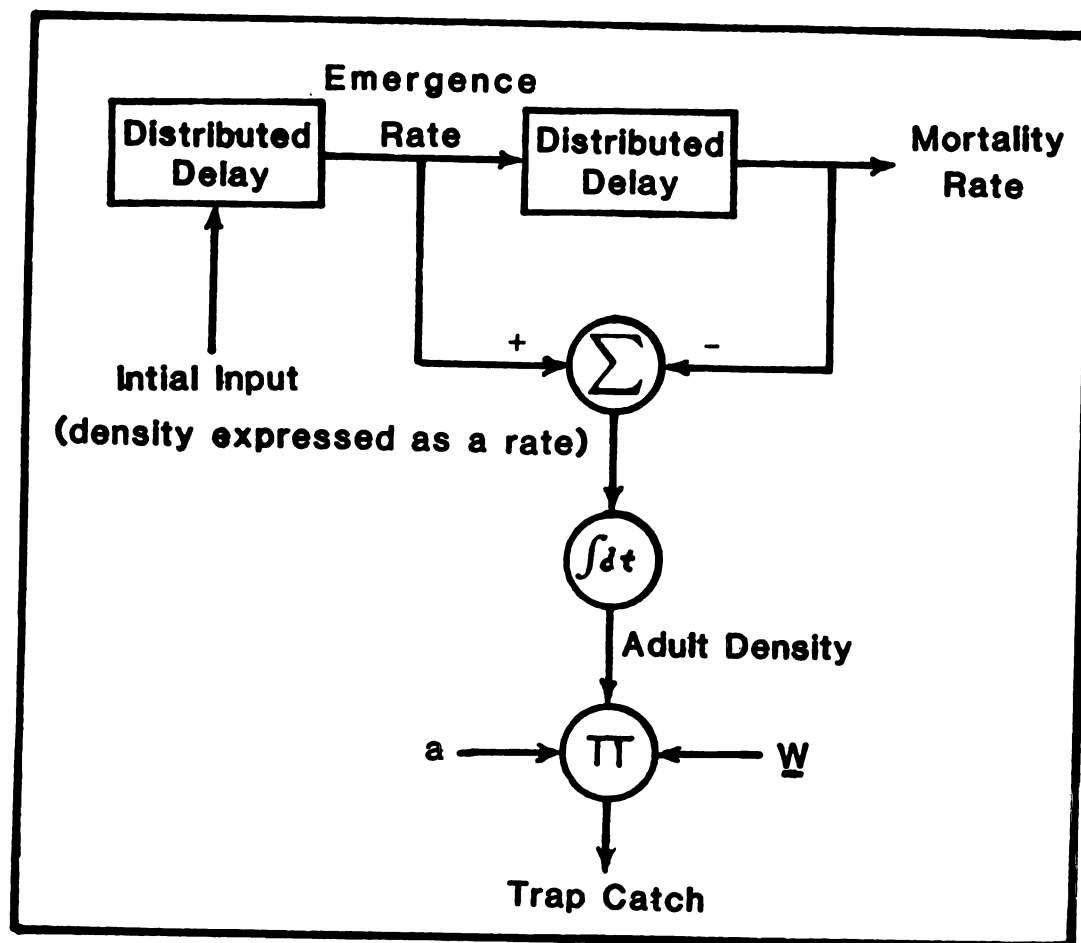


Figure 6. General structure of the model used to analyze the temporal distribution of malaise trap catches of *Glypta fumiferanae*. $\underline{W}$ is a vector of weather variables and a is a proportionality constant.

prior to determining the other model parameters until a best fit was obtained. k was estimated independent of the optimization because it must be an integer and the optimization algorithm used requires continuous decision variables. The mean of PTD ($\underline{PTD}$) and k are sufficient statistics for $f(\underline{PTD})$.

Variables in the set $\underline{W}$ included rainfall, relative humidity, temperature, and barometric pressure. Hourly measures of these variables were averaged over 800 to 2200 hours, which was the period G. fumiferanae was active. The values of $\underline{W}$ and $\underline{TC}$ used in the model are constant for a given day while $\underline{Ad}$ changes continuously according to the degree days accumulated on that date. Therefore, the value of $\underline{Ad}$ midway through a day was used in the function $\underline{TC} = f(\underline{Ad}, \underline{Aa})$.

To estimate model parameters, a linear form of (1) was adopted. Predicted trap catch is therefore given by:

$$\hat{TC}_n = (a + \underline{b}\underline{W}) \left(\int_0^{t_n} p(v) - \int_0^{t_n} f(t_n - z)p(z)dz dv \right)$$

where: n is a daily index, t_n are degree days accumulated on day n , and underlined variables denote vectors. The parameters a , $\underline{b}$ and $\underline{PTD}$ of the mortality rate were estimated using the complex nonlinear optimization algorithm due to Box (Kuester and Mize 1973). The objective function for the optimization is given by:

$$\text{Minimize } F = \sum_{n=1}^m (\hat{TC}_n - TC_n)^2$$

With this objective function, the value assigned to the parameters of a particular model minimizes a sum of squares about the observed trap catch.

Owing to the importance of the female parasitoid, the model was parameterized for female trap catch only. To initiate parameter estimation, the initial input (i.e., total number of pupal female parasitoids) was arbitrarily selected. This was done for two reasons. First, the absolute number of pupal G.

fumiferanae in the trapping area was not known. Second, we were interested in the qualitative aspects of the model, and knowing this value was therefore unnecessary. As a result, model parameters except PTD are scaled by the initial input.

As stated previously, the emergence rate $p(t)$ was determined from emergence data. The rate of adult female emergence was separated from the male emergence rate by assuming that the initial trap catch of females indicated the onset of female emergence and that the shape of the female emergence curve was similar to the joint male and female emergence curve. The first assumption is based on the fact that G. fumiferanae was not collected in any habitat other than the forest canopy. Hence, it is unlikely that females emerged at the same time as males but initially used a habitat other than the trees containing budworm in order to find food or alternative hosts. Parameters for the distributed delay used to describe female emergence were selected so that predicted emergence resembled the combined male and female curve but was appropriately delayed in time (fig. 7).

Results of the parameter estimation are given in table 1. Only models which had some ability to predict trap catch are presented. Since the objective function for the optimization process can be thought of as a residual sum of squares, an R^2 was computed for each model. A test of significance cannot be made, though, due to correlation among variables within the model and because the distribution of the various sum of squares is unknown. The best prediction of trap catch was achieved with precipitation and temperature as independent variables. Wet and cool weather was associated with declines in trap catch. Reasonably large changes in the residual sum of squares associated with the

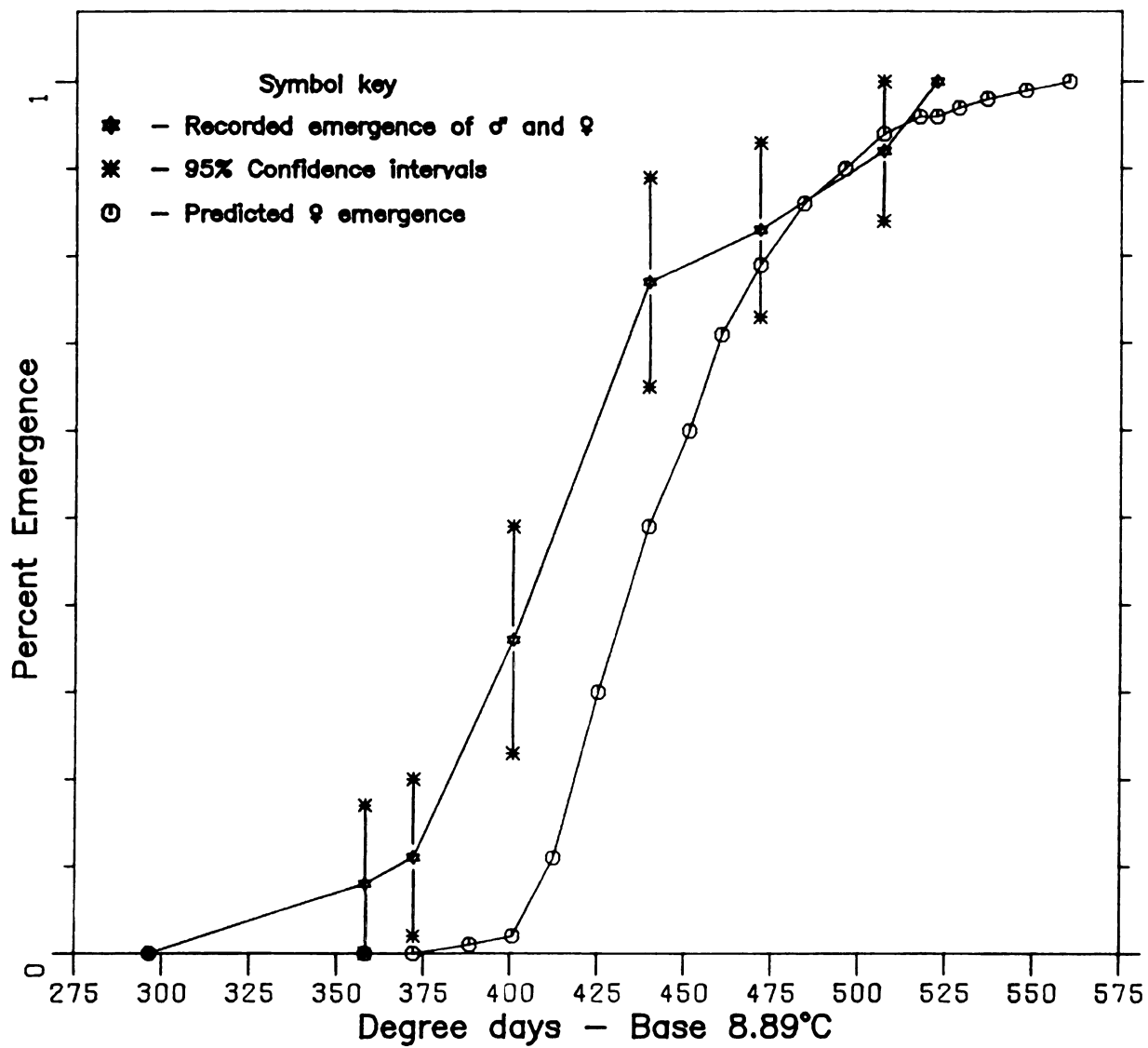


Figure 7. Observed combined emergence of adult male and female Glypta fumiferanae in stand 2 and predicted emergence of female G. fumiferanae as a function of degree days base 8.89 °C.

Table 1. Models used to predict the temporal distribution of malaise trap catch of female Glypta fumiferanae. Variables used are:

TC_n = predicted trap catch

T_n = average temperature between 800 and 2200 hours on day n

RH_n = average relative humidity between 800 and 2200 hours on day n

R_n = rainfall in inches between 800 and 2200 hours on day n

Ad_n = a measure of adult female density on day n

PTD_p = expected number of degree days for emergence from pupae from an initial time point t_o

PTD = expected adult female life span in degree days

K_p, K_m = shape parameters of gamma density function used to describe PTD

In all models the emergence rate is given by a distributed delay with $PTD = 55.5$, $k_p = 4$ and $t_o = 388$ degree days base $8.89^\circ C$.

The value of k_m was 8.

MODEL	$\overline{PTD}_m$	Residual Sum of Squares	R^2
1 $TC_n = .605 Ad_n$	81	1300	.51
2 $TC_n = (.012 + .852 T_n) Ad_n$	84	1117	.58
3 $TC_n = (1.24 - .892 RH_n) Ad_n$	76	1046	.61
4 $TC_n = (154.6 - 1.89 R_n) Ad_n$	86	708	.74
5 $TC_n = (.662 - .714 RH_n + .599 T_n) Ad_n$	87	982	.63
6 $TC_n = (.029 - 1.232 R_n + .9553 T_n) Ad_n$	87	546	.80

stepwise inclusion of each variable in this model ensured that the model was not over-parameterized. The predicted trap catch and predicted temporal distribution of adult females using this model and actual trap catch for stand 2 are shown in figure 8. The predicted temporal distribution of adults corresponds to the index of adult density.

As stated above, it was not possible to evaluate the statistical significance of the relationship between wet and cool weather and diminished trap catch. Nonetheless, one is led to the conclusion that the relationship is not spurious for two reasons. First, the probability of obtaining the relationship by chance is very small. Based on the model-generated population index, adult female G. fumiferanae were most abundant between 450 DD and 560 DD. At the same time, there were 3 days when trap catch was greatly reduced (517 DD, 522 DD, 560 DD) and 1 day when trap catch was somewhat reduced (484 DD).

The trap catch at 528 DD was not considered a reduced level even though in stand 2 the number caught on this day (18) was approximately the same as that caught at 484 DD (16). The reasons for excluding this date are twofold. First, in stand 3 the number caught on this date is close to the average number trapped during what we assume to be favorable weather conditions. Second, the trap catch on this date followed a period of extremely depressed parasitoid activity and the resumption of higher levels of activity may not occur immediately after the restoration of favorable environmental conditions.

During the four days of reduced trap catch and only during these days was precipitation recorded. In addition, for the three days with greatly reduced trap catch the temperature was lower than the average for the 12-day period. For the purpose at hand, these weather conditions will be classified as wet and cool.

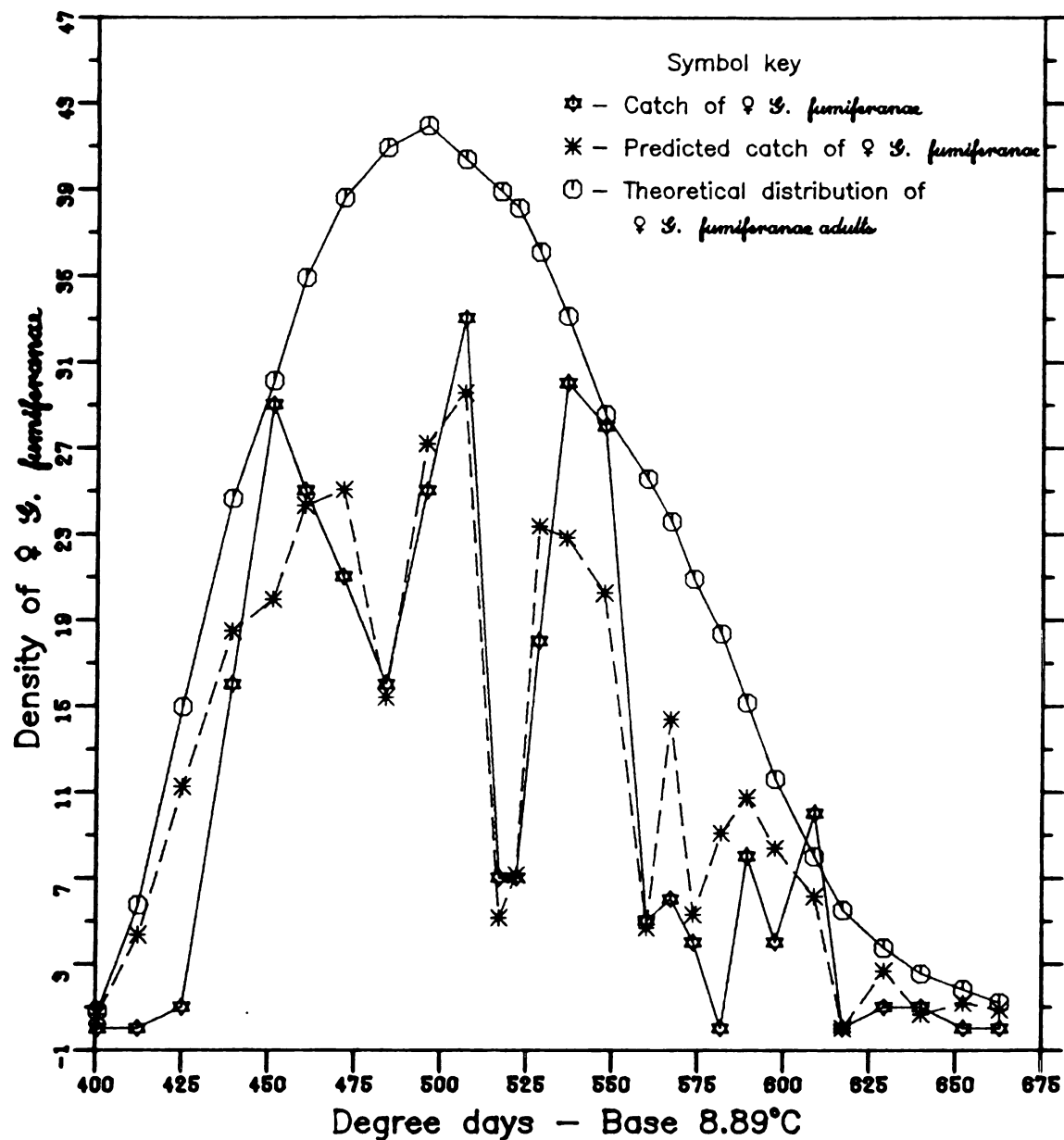


Figure 8. Predicted and actual malaise trap catch of adult female *Glypta fumiferanae* in stand 2 and the theoretical, relative temporal distribution of adult females. Malaise traps were located singly in 13 balsam fir trees.

A measure of the likelihood that no relationship exists between trap catch and wet, cool weather can be computed by determining the probability that these two sets of events occurred on the same days by chance.

The number of ways in which 4 depressed trap catches can be distributed among 12 days without respect to order is given by the binomial coefficient $\binom{12}{4}$. Suppose only the 3 days with greatly reduced trap catch are classified as low catch days and the other as a normal catch day. There then occurred 3 wet and cool days during which trap catch was reduced and 1 wet and cool day during which no reduction in trap catch occurred. The probability of this happening by chance is given by $\binom{4}{3} \binom{8}{1} / \binom{12}{4} = .065$. The probability of either this event or the more extreme event that all 4 days are classified as reduced is realized is then given by $.065 + \binom{4}{4} \binom{8}{0} / \binom{12}{4} = .067$. In contrast, the most likely single outcome would be for 1 reduced trap catch day to occur during the 4 wet and cool days and the rest to occur during the other 8 days ($p=.453$). Clearly, the probability that the partitioning of wet and cool days with reduced trap catch occurred by chance is very low. It is therefore likely that a relationship does exist.

The second reason for believing that the relationship between weather and trap catch is not spurious is that the model closely predicts the actual trap catch in stand 3 (fig. 9). Recall that the data from this stand was not used to parameterize the model. In this case, the initial input of pupal parasitoids was set equal to the input from stand 2 scaled by the ratio of estimated pupal densities in stands 3 and 2. The close fit of the model is not surprising considering the similarity in the trap catch from stands 2 and 3. What the relationship between the model and data from stand 3 does is reinforce the important fact that the trap catch from structurally different and spatially separated forest stands was strongly influenced by the same weather patterns.

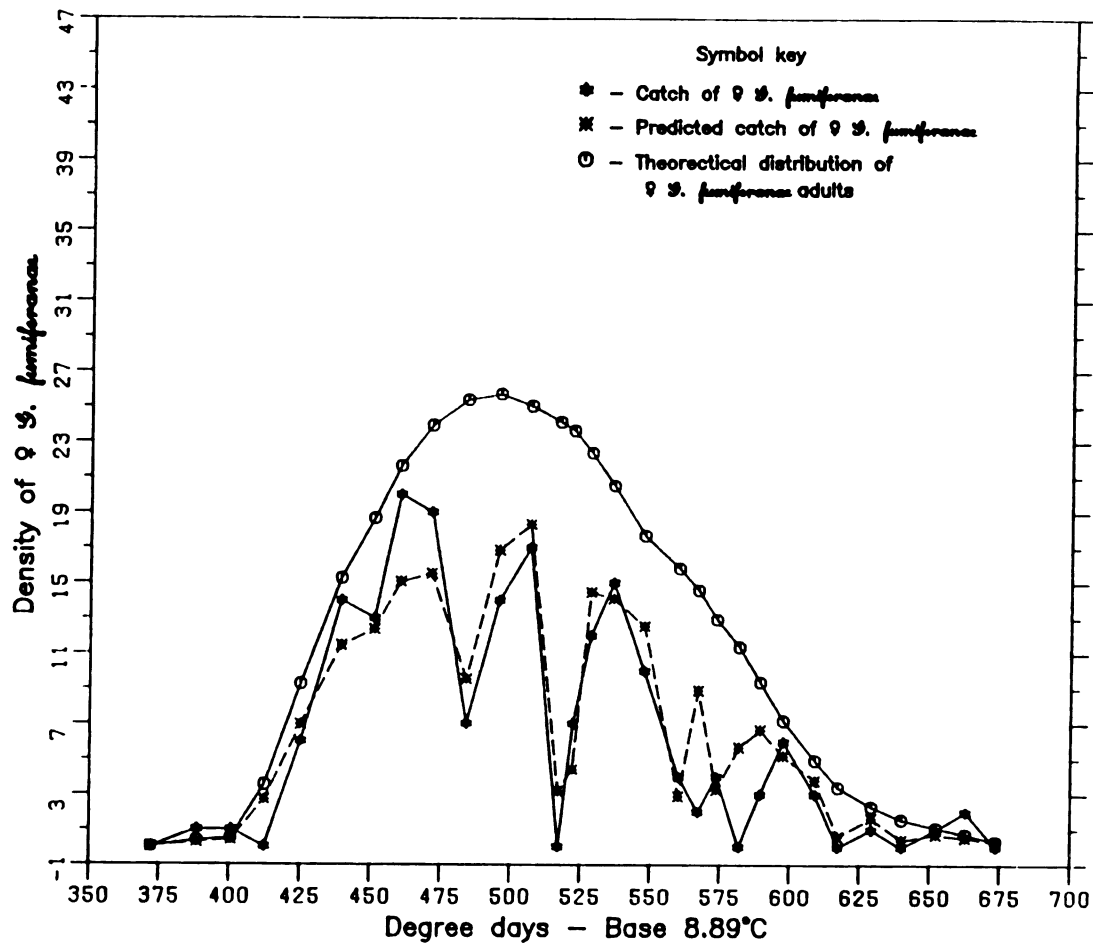


Figure 9. Predicted and actual malaise trap catch of adult female *Glypta fumiferanae* in stand 3 and the theoretical, relative temporal distribution of adult females. Malaise traps were located singly in 13 balsam fir trees.

We have established the fact that rainfall and cool temperatures reduce the malaise trap catch of G. fumiferanae. An important question is whether the reduced trap catch is indicative of a reduction or cessation of host searching. Based on observations of G. fumiferanae's host searching behavior made in 1981, the answer is yes. These observations will be discussed more fully later; however, two aspects are relevant here. First, very few G. fumiferanae were observed attacking hosts on cool, wet days. Second, the parasitoid frequently flew from one part of the tree to another when searching for hosts. This was especially evident when the parasitoids failed to discover hosts in a particular location. Since malaise traps are passive traps, trap catch will increase with activity of the parasitoid; in this case, activity is closely tied to host searching.

The estimated mean and variance of the lifespan of adult G. fumiferanae is given by the mean and variance of the gamma density function used to describe the physiological time delay between pupation and death of the adult parasitoid. The mean is $\text{PTD} = 87 \text{ DD}$ and the variance is $(\text{PTD})^2/k = 946 \text{ DD}$. The mean corresponds to ca. 10.5 days in 1981. A similar lifespan was evident in 1980. This conclusion is based on the fact that the degree day interval during which female parasitoids were trapped in 1980 is approximately the same as that in 1981.

In the laboratory, we found that adult female G. fumiferanae died within 3 days if they were not fed. This implies that in the natural environment, adult G. fumiferanae do indeed feed. They do not, however, use the vegetation on the forest floor as a food source. This assertion is based on two observations. First, although many parasitoids were caught in malaise traps on the forest floor, no G. fumiferanae were snared. Second, extensive sweep-netting of the ground

vegetation failed to reveal the presence of G. fumiferanae. While it is evident that the adult parasitoids do feed, they apparently do so in the forest canopy. Furthermore, forest composition appears to have no influence on the parasitoids' ability to secure food. This is founded on the equivalence of the parasitoid lifespans in stands 2 and 3, and the fact that stand 2 was exclusively balsam fir and stand 3 a mixture of balsam fir and other coniferous and deciduous trees.

Laboratory Study: In the laboratory, we sought to elucidate whether a temperature and light intensity gradient influenced G. fumiferanae's host searching behavior. The study was catalyzed by the theory of optimal foraging and information which indicated that G. fumiferanae searched for hosts in what would appear to be a non-optimal fashion.

It is realistic to assume that parasitoids adopt host searching behaviors which maximize the number of hosts parasitized at the end of their lifetime. Natural selection will favor those strategies which result in a reproductively efficient distribution of the parasitoids' offspring among available hosts. Most hosts of parasitoids are distributed in a non-random fashion and often in patches of variable density. Theoretical and laboratory investigations of parasitoid host searching (Royama 1970, Cook and Hubbard 1977, Hubbard and Cook 1978, Waage 1979, Nachman 1981) and general foraging strategies (Charnov 1976; Parker and Stuart 1976; Pyke, Pullman and Charnov 1977) have led to the principle of optimal patch use. Briefly, this means that all patches of the resource are reduced to some common harvesting rate. Thus, if a parasitoid's rate of encounter with healthy hosts is to be maximized over the period of time during which hosts are available, then the optimal solution requires that when presented with host patches of different density, the parasitoid will reduce all the areas it uses to the same rate of encounter between itself and healthy hosts.

The distribution of 159 attacks by G. fumiferanae on budworm observed in the field is given in table 2. Observations were made by individuals positioned in tree crowns who recorded the activity of individual female G. fumiferanae. The length of time that a particular parasitoid was observed varied from 30 seconds to over 45 minutes. More attacks were observed in the outer portion of the tree crown than on the interior. This distribution may be biased since parasitoids in different parts of the trees may be more easily detected. However, because the observer was positioned within the tree crown, this bias should have deflated the number of attacks observed in the exterior part of the crown.

According to an optimal foraging strategy, an approximately equal distribution of attacks between the exterior and interior portions of the crown would be expected if the hosts were equally distributed in these two areas. This is not the case, though. Lewis (1960) found that only 25% of the hibernating budworm population were found on the terminal 15-inch twigs of whole branches sampled from balsam fir. He also found a trend of increasing parasitism by G. fumiferanae on the exterior of the crown. Obviously, G. fumiferanae responds to factors other than the host distribution when searching for hosts. The following experiment was conducted to determine if physical factors associated with the interior and exterior of the tree crown influenced the parasitoids' host searching behavior.

A chamber was constructed in which: (1) a temperature and light gradient could be generated and (2) parasitoids would be free to range over this environmental spectrum for hosts. The chamber was a rectangular tube of dimensions 80 x 10 x 10 cm and was manufactured from plexiglass 1.2 cm thick. On the outside walls of the chamber, 5 series of two 25 watt, 725 ohm heat dissipating resistors were mounted and wired in parallel. A controller, which

Table 2. Distribution of attacks by Glypta fumiferanae on spruce budworm larvae in balsam fir trees (n = 16). The exterior of the tree denotes the first 18 inches of the canopy.

Location of Attack							
EXTERIOR				INTERIOR			
Bud Tip	Lichen	Bark Scale or Branch Fork	Flower Bract or Needle Base	Bud Tip	Lichen	Bark Scale or Branch Fork	Flower Bract or Needle Base
ATTACKS							
39	13	14	27	3	21	35	10
Total		93				69	
		57%				43%	

produced pulses of electricity whose duration were regulated by potentiometers, was connected to each set of resistors. Pulses of different durations were distributed among the five sets of resistors, resulting in differential warming of the chamber. A circuit diagram for the controller is provided in appendix 2.

The chamber was placed in a constantly cooled (10°C) and darkened room and illuminated from above by two 30 watt fluorescent bulbs. The experiments were conducted in the cooled room in order to obtain the desired temperatures within the chamber and so that the chamber would not have to be recalibrated due to changes in room temperature. The light intensity in selected portions of the chamber was regulated by placing a piece of Saran® 20-mesh screening over these sections.

G. fumiferanae pupae were collected and males and females reared at 22°C and a 14 hour light/8 hour dark photoperiod. To provide hosts for G. fumiferanae, budworm pupae were collected and reared, and adult males and females were placed in small paper bags on which the females oviposited. Eggs were collected and placed in a petri dish which was then covered with gauze and Parafilm®. The dishes were placed in a paper sleeve in which an opening was cut to allow light to pass through the gauze and Parafilm. When the eggs hatched, the photopositive larvae crawled onto the gauze and spun hibernaculae.

Parasitoids used in the experiment were between 3 and 6 days old. This age range was imposed to avoid confounding results with age-dependent behavior. In addition, all experiments were conducted between 1100 and 1400 hours to eliminate the possibility of diel periodicity as a source of variation. Ideally, the influence of temperature and light on the behavior of female G. fumiferanae should have been studied independently and then jointly. However, the short time in which adult G. fumiferanae were available precluded such an approach.

A temperature and light gradient was arranged so that there was a fully illuminated warm environment, a shaded cool environment, and a spectrum between these limits (table 3). Four patches of gauze, each with five budworm hibernaculae, were placed in two warm and light regions and two cool and shaded regions. No hibernaculae were placed in the center cell into which female parasitoids were introduced. After the parasitoids moved at least one cell away from the entry point, their behavior was recorded for 1 to 1-1/2 hours. This consisted of recording the time intervals each parasitoid spent in each environment searching for hosts, attacking hosts, and resting. The number of ovipositions in each cell was also recorded. Searching behavior consisted of G. fumiferanae probing and examining the gauze and surrounding areas with its antennae in an effort to locate hosts. Attack behavior consisted of probing with the ovipositor and oviposition. It was possible to determine when oviposition occurred, as the females, upon inserting the ovipositor in the host, remained completely motionless for ca. 15 seconds. Resting behavior consisted of immobility, preening, and non-directed movement.

The average total time spent, average time spent attacking hosts, and average time spent not attacking hosts in each of the different environmental conditions is given in table 3. Attack time consisted of both attack and searching behavior, when searching behavior occurred between attacks separated by a short time interval. Attack time for the two warm-light and cool-shaded environments were summed. This was done because few attacks occurred in the cells at the extreme end of the chamber and this result cannot be attributed to environmental conditions. It is just as likely that most attacks occurred in the cells closest to the entry because this is where hosts were first encountered.

Table 3. Total time and time spent in attack and non-attack behavior by *Glypta fumiferanae* in different environmental regimes. Time is in minutes and tenths of minutes. The variable W is the number of cases (C_i) in which time spent in cell 4 is greater than that in cell 2 when parasitoids were observed in either of these cells. ϕ is the probability that $w \leq W$ given that $W/\Sigma C_i = 0.50$. Attack times in cells 1 and 2 and in 4 and 5 are summed.

Cell	Environmental Conditions						
	1	2	3	4	5		
Temperature °C	31	27	22	19	15		
Lighting	F U L L / P A R T I A L						
Hosts present	yes	yes	no	yes	yes	ΣC_i	ϕ
Total time n = 23							
Mean	8.29	26.76	11.49	7.24	5.16		
Std. Dev.	13.78	21.00	12.90	17.00	13.43		
W				4		23	.001
Non-attack time n = 21							
Mean	7.81	13.37	11.49	1.68	2.37		
Std. Dev.	13.93	12.86	12.90	3.16	7.15		
W				4		21	.004
Attack time n = 14							
Mean	28.05			12.77			
Std. Dev.	23.05			19.53			
W				5		14	.212

Analysis of the data is confined to observations from cells 2 and 4, except for attack time in which the data is summed for cells 1 and 2 and for cells 4 and 5. Reasons for this restriction are as follows: The center cell (3) was not included because hosts were not placed in this region. The cells at the ends of the chamber (1 and 5) were not included since the conditional probabilities for a parasite to enter these cells, regardless of environmental influences, are not the same as those for cells 2 and 4. This is a result of the linear arrangement of the environments.

Since independence and normality assumptions could not be met, the following method of analysis was used. Let T_i be the time a parasitoid spends in cell i . Let $v = 1$ if $T_2 > T_4$ and $v = 0$ if $T_4 < T_2$. Define W as $\sum v$. Then W is distributed as a binomial random variable. If the time spent in cells 2 and 4 were the same, then the parameter p of this binomial distribution would equal 0.5. The probabilities of obtaining the observed or more extreme values of W with the hypothesis that p equals 0.5 are given in table 3. These probabilities are very low for total time and non-attack time; hence, the null hypothesis is rejected. The value of a more extreme value of W for attack time has approximately a 1 in 5 chance of occurring, given $p = 0.5$. Hence, the null hypothesis cannot be outright rejected; however, there is an indication that differences exist. A more definitive analysis of the allocation of attacks can be made by considering the distribution of ovipositions. In cells 1 and 2, 258 ovipositions were recorded; in cells 4 and 5, 154 were recorded. If temperature and light produced no effect on the oviposition distribution, the proportion of attacks in cells 1 and 2 should be 0.5. The actual proportion was significantly different from this value (normal approximation, $\alpha < .001$).

The data suggests that the distribution of attacks by G. fumiferanae observed in the tree are a result of the light and/or temperature differential which exists between the interior and exterior of the tree crown. If temperature does play a role, it is due to increased radiant heat since only a very small ambient temperature differential would exist between the interior and exterior of the crown.

Historical Data: Based on the field studies of G. fumiferanae's activity patterns, we concluded that wet and cool weather would inhibit the parasitoid's searching efficiency. In this section, this relationship is explored further by examining historical data on the interaction between the parasitoid and its host.

Extensive data on this interaction was collected from 1950 to 1958 during the Green River Project in northwestern New Brunswick. Details of the study can be found in Morris (1963). This data has previously been analyzed by Miller (1960) who also thought that rainfall might influence the attack efficiency of G. fumiferanae. He did not, however, examine this in detail. Furthermore, Miller employed a specific model to describe the attack dynamics of the parasitoid. In contrast, we have analyzed the Green River data without the encumbrance of a particular parasitoid attack model by exploring the relationship between the ratio of hosts to parasitoids (H/P), rainfall, and percentage of hosts parasitized. In this case, this is a better approach since no a priori assumptions about parasitoid searching behavior are necessary. The influence of temperature on attack efficiency was not explored because the data lacked the resolution necessary to evaluate this factor.

Original data on spruce budworm densities and on the rate of budworm parasitism by G. fumiferanae in the years 1950 to 1958 at the Green River field

station was obtained from the Maritime's Forest Research Center, Fredericton, New Brunswick. The data from 3 plots (G2, G4, G5) were selected for use in the analysis based on the plots having a data series spanning 5 or more years, having budworm densities relatively constant, and having no appreciable tree mortality. The latter two criteria were established to minimize the possible influence of changes in the host's density and distribution and of changes in the forest environment on the parasitoid's searching behavior.

Parasitism rates had been determined by dissecting samples of third and fourth instar budworm. These rates were employed as an index of the parasitism of second instar budworm, which is the host stage G. fumiferanae attacks. The use of this index, however, does introduce a potentially large bias into the estimates of parasitism. Between the second and third instars, budworm undergo dispersal during which a large number of insects die. The propensity for dispersal is lower for parasitized larvae than for unparasitized ones (Lewis 1960). As a result, depending on the differences between the dispersal rates of parasitized and unparasitized larvae, assessment of parasitism in the spring will be inflated over the true parasitism rate. This would not be a problem if this inflation did not vary from year to year. Unfortunately, such an assumption cannot be met.

Two factors influence the proportion of third instars lost during dispersal: stand composition and weather (Kemp et al. 1980). Stand composition did not change in the plots from which the data was collected. Weather, on the other hand, was a dynamic variable. Results from a simulation model indicate that the proportion of third instars lost during dispersal might vary by as much as a factor of 2 between years as a result of weather conditions during the dispersal period (Kemp et al. 1980). The net result is that the apparent parasitism rate may

change dramatically from one year to another while the actual rate changes little. There is no way to determine this bias; however, one must be cognizant of the potential error.

An index of the density per 10 m² foliage of female G. fumiferanae was computed by first assuming that the survival of the parasitoid from the larval stage located in the budworm to the adult stage was time invariant and that the sex ratio of G. fumiferanae was also time invariant. The index was then determined by multiplying the density of third and fourth instar budworm by one-half the parasitism rate.

The index of host density (second instars) was based on egg counts less egg mortality and a constant dispersal loss of first instars. An assumption of a constant first instar dispersal loss is supported by references contained in and the simulation results obtained by Kemp et al. (1980).

To determine rainfall during the flight period of the females, the approximate calendar dates over which this activity occurred were determined by assuming that the occurrence of the female parasitoids flight activity with respect to degree days would be the same in northwestern New Brunswick as it was in Michigan. The time period of activity in Michigan was determined from the malaise trap catches of 1980 and 1981. Minimum and maximum degree day values for which females were caught for these two years were 388.44 and 662.88. However, the magnitude of activity was not uniform over this interval. Hence, total precipitation for the interval 428 DD - 584 DD was computed since it was during this period that peak activity occurred. The dates and precipitation for this interval during the years 1950 to 1957 in the Green River area are given in table 4.

Table 4. Julian dates for the degree day interval 428 - 584 (base 8.89°C) and precipitation during this period in the years 1950 to 1957 at the Green River field station, New Brunswick.

<u>Year</u>	<u>Julian Dates</u>	<u>Precipitation in inches</u>
1950	215 - 244	2.87
1951	216 - 240	3.07
1952	203 - 221	2.57
1953	204 - 232	2.00
1954	214 - 241	5.87
1955	203 - 225	2.79
1956	221 - 248	3.00
1957	217 - 245	0.70

The data from each plot is presented in figure 10. Note that the percentage of hosts attacked in year i is plotted at year $i + 1$. This was done to preserve the temporal sequence in which the data was collected; the parasitoid searched for and attacked hosts in late summer while the assessment of this attack was completed in early spring the following years. Of particular interest is the year 1954. During this year the host density declined, the parasitoid density increased, and parasitism declined dramatically in all three plots. This decline in the parasitism rate is contradictory to what would be expected. However, during 1954, more precipitation fell than in any other year. Because the decline in parasitism was evident in all three geographically separated plots, it is logical to conclude that the decline was in fact related to inordinate rainfall.

A more complete picture of the relationship between rainfall and parasitism is obtained by using the data from all 3 plots to generate a parasitism surface as a function of the H/P ratio and rainfall (fig. 11). The pronounced influence of rainfall on the parasitism rate is readily apparent at both high and low H/P ratios. There are, however, two unexplainable irregularities in the parasitism surface. With moderate rainfall and high H/P ratios, a distinct valley exists when the parasitism rate should either be nondecreasing or nonincreasing with respect to the independent variables. There is also a lack of response in the parasitism rate to a decline in the H/P ratio when associated with a moderate to high rainfall. It must be remembered, though, that the data used in the analysis is subject to a great deal of potential bias. This bias may be due to the affect of spring dispersal on the measured parasitism rate and also due to year-to-year differences in the temporal synchrony between G. fumiferanae and the budworm

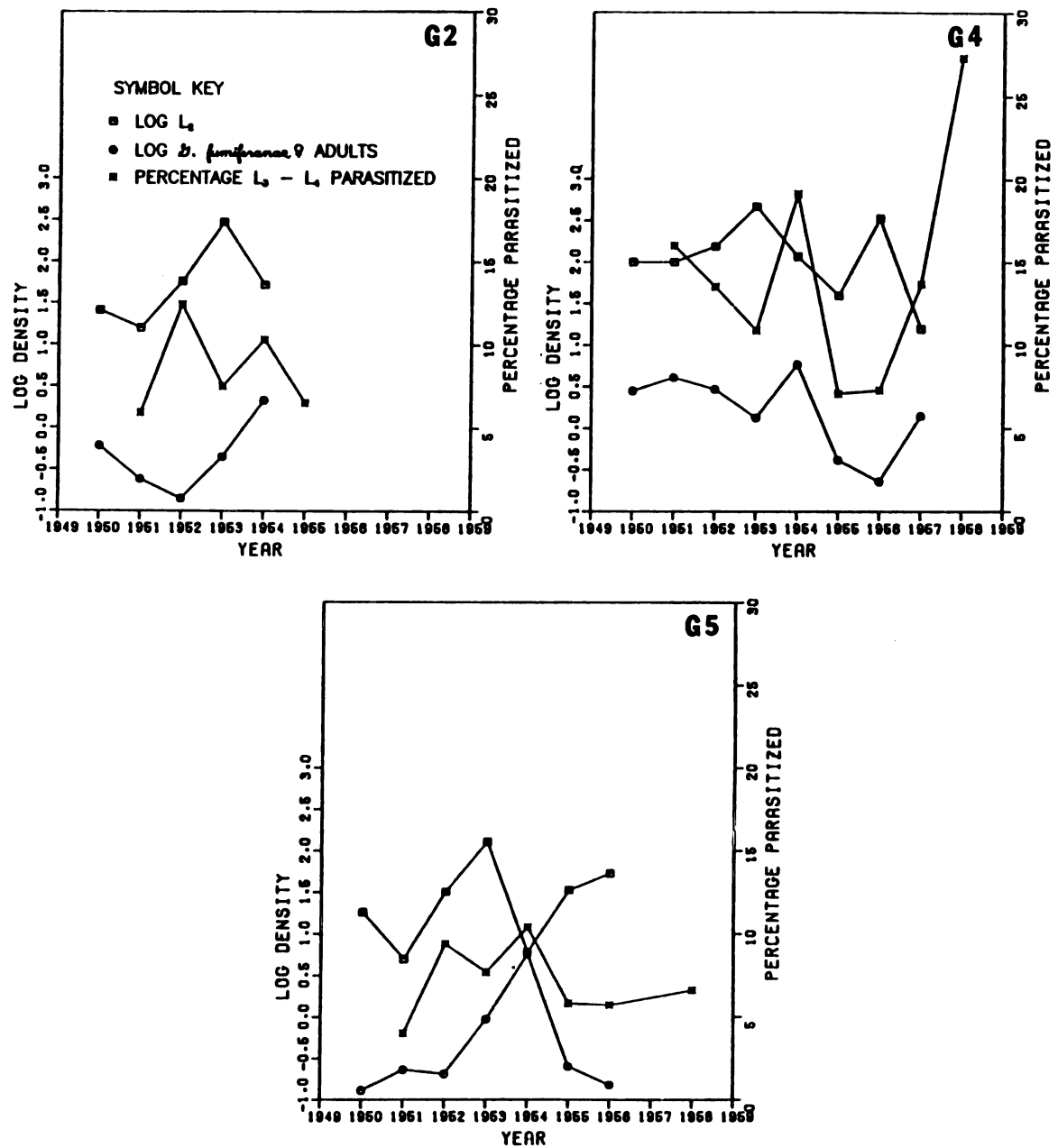


Figure 10. Temporal relationships between the density per 10 m² foliage of second instar (L_2) spruce budworm, the density of adult female *Glypta fumiferanae* and the percentage of third and fourth instar (L_3-L_4) budworm parasitized by *G. fumiferanae* in three plots at the Green River field station, New Brunswick. (Data obtained from Maritimes Forest Research Center Fredericton, New Brunswick)

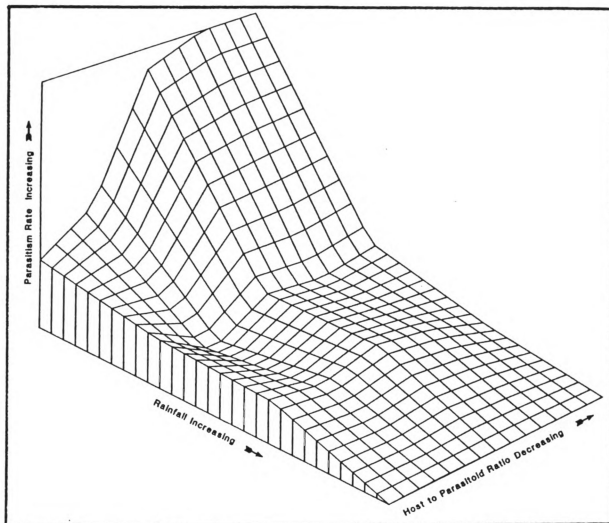


Figure 11. Parasitism of spruce budworm larvae by *Glypta fumiferanae* as a function of the ratio of hosts to parasitoids and rainfall during the period of adult parasitoid activity.

host. In addition, a large amount of sampling variability must be present, although information on this variability is unavailable. Finally, temperature has not been included as an independent variable even though it has been shown to influence the activity of the female parasitoid. It is somewhat surprising that any discernable relationship between rainfall and parasitism was produced. In fact, in order to be visible, the relationship must be quite strong. When this relationship is combined with the observation that rainfall impedes host searching by the parasitoid, a conclusion can be drawn that excessive rainfall greatly diminishes the attack efficiency of the parasitoid.

Discussion

Factors other than the host which influence the number and distribution of hosts attacked by a parasitoid may be classified as being either controllable or uncontrollable. Controllable factors are those which can be ameliorated or accentuated by management actions. In this study we have identified two ways in which uncontrollable factors affect G. fumiferanae. First, the attack efficiency of the parasitoid is greatly diminished by excessive rainfall and/or cool temperatures. This is because host searching by the parasitoid occurs at a reduced rate during these weather conditions. Second, the spatial pattern of host searching by G. fumiferanae is influenced by light intensity and/or temperature. Similar types of phenomena have been observed for other parasitoids.

Temperature, sunlight, rainfall, and dew have been reported as influencing the ability of parasitoids to locate and parasitize hosts. Klomp (1959) found that the attack efficiency of the tachinid parasitoid, Carelia obesa, was correlated with the amount of sunshine during the period of egg deposition. Burnett (1951,

1954, 1958) demonstrated that as the temperature declined, the number of sawfly pupae attacked by a chalcid parasitoid decreased. This decrease was attributable to a decline in the capacity of the parasitoid for oviposition and also to a reduction of the number of hosts contacted by the insect. In field experiments, he noted that parasitism was inhibited by rain and heavy dew. Messenger (1968) found that temperature extremes affected the aphid parasitoid, Praon exsoletum, by inducing a shift in the proportion of ovipositional activities relative to other activities engaged in by the females, and by reducing the proportion of successful attacks. In laboratory studies of Bracon mellitor, Barfield et al. (1977) found that the parasitoid exhibited a narrow temperature range in which total fecundity was maximized.

The spatial interplay between parasitoid host searching and abiotic factors has also been observed before. Weseloh (1976) reviews a number of studies which indicate that responses to humidity, light, and temperature are at least partially responsible for the spatial distribution of parasitoids in forest habitats. Munster-Swendsen (1980) has suggested that the aggregation of the parasitoid Apanteles tedellae with respect to its host may be explained by an evolution of a similar preference for physical conditions as opposed to a direct response to host densities.

An important factor influencing adult parasitoids and, one that may be controllable, is the availability of nutrients and moisture. These resources are essential for the survival of many adult parasitoids (Townes 1958, Hassan 1967). We found no evidence that a particular habitat was a better source of nutrients or moisture for G. fumiferanae. Examples exist, however, which demonstrate the importance of habitat in providing food sources for adult parasitoids (e.g., Syme 1975, Calderon 1977).

The importance of abiotic and biotic factors other than the host in determining the number and distribution of hosts attacked is clear. As a result, it is desirable to know, at least in a qualitative manner, how these factors influence the dynamics of parasitoid-host systems and the capacity of a parasitoid to act as a biological control agent. One way of elucidating these influences is to incorporate these factors, in a general way, in the mathematical models used to describe and study these systems. This is done below.

The dynamics of coupled parasitoid-host systems with discrete generations have been extensively analyzed with the following model:

$$H_{t+1} = H_t F(H_t) f(H_t, P_t) \quad (2)$$

$$P_{t+1} = H_t (1 - f(H_t, P_t))$$

Because the basic structure of this model corresponds to many real-world systems, it will serve as a basis for the discussion. In (2), H_t and P_t are host and parasitoid densities, $F(H_t)$ is the net rate of increase of the host in the absence of P_t , and $f(H_t, P_t)$ is a parasitoid attack function. This function can be interpreted as the probability of H_t hosts escaping discovery and subsequent parasitization by P_t parasitoids.

Model (2) is nonlinear. As a result, analytical analysis is generally limited to determination of the equilibrium states and stability properties of these states. Equilibrium states are values of state variables which are either constant or are periodic through time. Periodic equilibrium states are called limit cycles. In (2), the state variables are the host and parasitoid densities. An equilibrium point or cycle is stable if, when a state variable is perturbed from its equilibrium, system dynamics drive the variable back to or asymptotically close to this state. An equilibria is locally stable if the magnitude of the perturbation

is restricted to some neighborhood about the equilibrium. It is globally stable if such a restriction is not necessary.

Limiting the analysis of (2) to determination of equilibria and stability of these equilibria is not overly restrictive because these properties convey, within the context of (2), the salient features of a successful biological control agent. These features are that a parasitoid can depress and/or help maintain a host population at a density well below the host's carrying capacity. This does not imply that the parasitoid must singularly be able to do this, since $F(H_t)$ may contain complex density dependent relations. What is necessary is that all mortality factors acting in combination are able to do so, and that in the absence of the parasitoid, regulation would not be possible or would not be as strong. The aim here is to examine the ties between factors which influence adult parasitoids in their search for hosts and the equilibrium states and stability properties of (2). This will be done by first relating the empirical observations to forms of (2) for which equilibria and stability have been laid bare. An analysis is then made of a variation of (2) which provides a different insight into the importance of factors influencing adult parasitoid dynamics.

A sufficient condition for stability in simple one parasitoid-one host models is that spatial or temporal incoincidence (or both) between the host and parasite occur¹ (Hassel 1978, Nachman and Munster-Swendsen 1978). A stable system is

¹Stability can also be generated if: (1) $F(H_t)$ is a nonlinear function such that the host is limited by the carrying capacity of its habitat (Beddington *et al.* 1975) or (2) the host and parasitoid populations are comprised of cells and dispersal of hosts and parasitoids occurs among these cells (Crowley 1981 and references therein). However, (1) results in host equilibrium densities which are unrealistically high (Beddington *et al.* 1978), and (2) might be considered as a component of spatial and/or temporal incoincidence.

generated when either of these events is realized at appropriate intensities. Stability transpires because the parasitoids do not over-exploit the host resource. Excessive incoincidence leads to runaway host populations while too little incoincidence leads to diverging oscillations in the host and parasitoid densities. Here, attention is restricted to spatial incoincidence.

Two factors lead to spatial incoincidence: (1) contagiously distributed hosts, and (2) parasitoids which forage in response to this patchy distribution and possibly also in response to other biotic and abiotic factors. The essential aspects of spatial incoincidence can be captured in (2) by incorporating non-random host searching by the parasitoid. This has been done a number of ways (Hassel and May 1974, Murdoch and Oaten 1975, Munster-Swendsen 1982). A detail independent and analytically tractable method first proposed by Griffiths and Holling (1969) and fully developed by May (1978) is used here.

May proved that the zero term of the negative binomial distribution

$$(1 - aP/k)^{-k} \quad (3)$$

could be used to model $f(H,P)$ when the hosts are patchily distributed and the parasitoids search randomly (i.e., do not discriminate previously attacked hosts) within a particular host patch. This is a descriptive model unlike other models which have been derived from the geometrical attributes of parasitism (Royama 1971). Nonetheless, it is adequate for our purposes because we are only interested in being able to describe the outcome of the parasitoids' attack.

In (3), the parameter (a) is an index of the searching efficiency of a parasitoid within a patch and k is an index of its aggregation with respect to the host distribution. Note that an unrealistic linear relationship between the number of hosts available and number attacked is assumed. In general, the

number of hosts attacked by a constant density of parasitoids must reach an asymptotic limit as host density increases (Holling 1959, Royama 1970). For the present, this additional complexity is omitted, although it will be discussed later.

May has shown that a sufficient condition for stability of an equilibrium of (2) employing (3) and allowing $F(H_t)$ to be a constant is $k < 1$. This means that a sufficient degree of aggregation must be realized for stability. Searching efficiency (a) has no influence on the stability of the equilibrium in the one parasitoid-one host model. It does, however, scale the equilibrium values.

Factors such as temperature, rainfall, and adult food sources which influence the searching efficiency of a parasitoid can be incorporated in (2) through the parameter (a). For instance, if adverse weather causes a reduction or cessation of host searching activity, this can be incorporated by writing (a) as (a't) where a' is an instantaneous index of searching efficiency and t is the amount of time favorable weather occurs. Likewise, those factors which influence the spatial distribution of parasitoids can be partially described in terms of k. They can only be partially described since k can only incorporate the influence of factors up to the point where the spatial distribution of parasitoid attack is random and because a single statistical parameter can not capture all aspects of a complex spatial pattern. Nonetheless, this simple model indicates that it is essential that parasitoid aggregation with respect to the host distribution not be interrupted by extrinsic factors if the parasitoid is to be an effective biological control agent. The model also indicates that factors which influence the searching efficiency of the parasitoid cannot alter system stability but simply influence the equilibrium densities. Similar conclusions can be made for all single parasitoid-single host models which incorporate non-random parasitoid search.

An important question is whether these models are representative of any real-world situation. We feel that they may describe cases of introduced pests and exotic parasitoids. Additional complexity is needed, though, to describe other, more common parasitoid-host systems. As demonstrated below, these added components dramatically alter the effect of factors that influence adult parasitoids on the stability properties of a particular system.

Populations of many insects exist for long periods of time at low densities and periodically erupt to high densities. This is most noticeable in temporally continuous and undisturbed ecosystems but may also occur in agro-ecosystems. The underlying mechanism of such phenomena is density dependent mortality which at first becomes more effective with increasing densities but whose effectiveness then diminishes beyond some threshold density. This model, often called a double equilibria population process, was proposed as an explanation of population dynamics by Ricker (1954), Morris (1963), and Takahashi (1964), and has been extensively reviewed by Holling (1973), May (1976), Royama (1977), and Berryman (1978). The salient features of the models are two equilibrium points or cycles, one at low densities which is locally stable, the other at higher densities which is unstable. A population will reside in the low density state until moved beyond the unstable point or until the unstable point is itself moved below the existing population density. Because these types of population processes are likely to be quite common, we have analyzed a form of (2) which incorporates such processes along with a parasitoid.

Consider a situation where a host population is limited by a group of factors which, when acting in combination, produce a double equilibrium population process. To add substance, let this group consist of predators whose density

is constant and which display a sigmoidal functional response and a parasitoid.

The predation can be incorporated in (2) by writing $F(H_t)$ as:

$$\delta \exp [(-\gamma P_b H_t) / (\alpha^2 + H_t^2)] \quad (4)$$

The parameter (δ) in (4) is the net rate of increase of H in the absence of parasitism and predation by P_b predators. The exponential function describes the probability of H prey escaping predation by these predators. It is based on Real's (1977) extension of models of enzyme kinetics for describing functional responses. The parameter (γ) is the maximum number of prey captured per predator, and α is the density of prey at which the predator's consumption level is $1/2 \gamma$.

The model obtained by incorporating (4) and (3) in (2) is:

$$H_{t+1} = H_t \delta \exp [-\gamma P_b H_t / (\alpha^2 + H_t^2)] (1 + aP/k)^{-k} \quad (5)$$

$$P_{t+1} = H_t [1 - (1 + aP/k)^{-k}]$$

Predation is assumed to occur after parasitism and is complementary.

In order to analyze (5), numerical procedures had to be adopted. These procedures consisted of: (1) evaluating equilibrium densities for a particular set of parameters via Newton's method for determining the roots of a function, (2) ascertaining the stability of these equilibria, and (3) determining a region of stability about each equilibrium point by iteratively perturbing equilibria and simulating system dynamics. Because numerical methods were necessary, it was impossible to completely elucidate model behavior. However, the results do indicate its qualitative properties.

Suppose that the predators by themselves are incapable of regulating the prey population. That is, the net recruitment curve in the absence of parasitism is greater than one for all prey densities (fig. 12). By incorporating a parasitoid

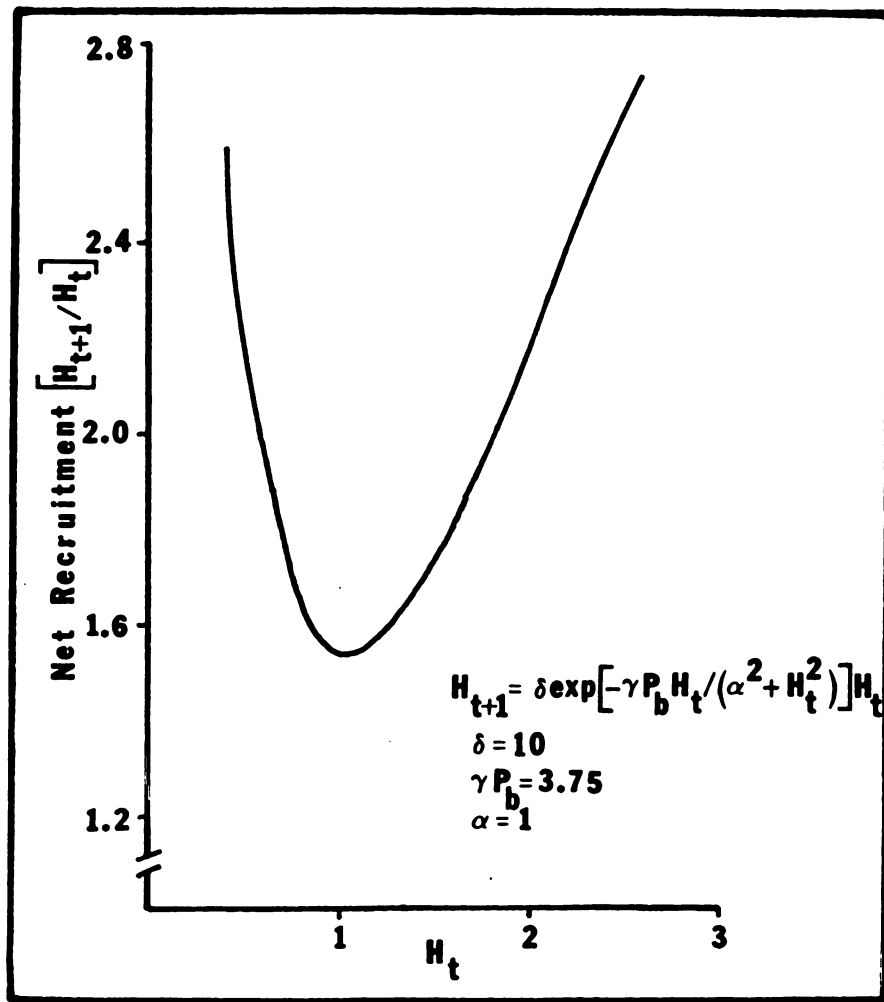


Figure 12. Net recruitment for an insect population preyed upon by a constant density of predators which exhibit a sigmoidal functional response. H is the insect density, P_b is the predator density, δ is the rate of increase of H , γ is the maximum number of H consumed by a predator and α is the density of H for which predator consumption is $\gamma/2$.

with an appropriate searching efficiency, a stable, low-density equilibrium can be generated. The requirement placed on the searching efficiency is that the host equilibrium falls in a particular region of the cusp of the recruitment curve.

The equilibrium densities of the parasitoid and host and eigenvalues of model (5) linearized about the equilibrium points for $\delta = 10$, $\gamma P_b = 3.75$, $\alpha = 1.0$, and various values of parasitoid searching efficiency and aggregation are presented in table 5. The methodology for obtaining these values is outlined in appendix 3. The eigenvalues indicate which equilibria are locally stable, since a necessary and sufficient condition for local stability of an equilibrium is that the real part of the eigenvalue has modulus less than 1.

The most noticeable aspect of this model is that aggregation is no longer necessary for local stability. Even with random parasitoid search ($k = \infty$), stable equilibria exist. Moreover, one measure of system resilience, the speed with which perturbed populations return to the vicinity of an equilibrium, is higher with less aggregated parasitoid search. System resilience is the ability of a system to absorb changes in state variables or parameters without abrupt changes in system trajectory. Here, system resilience relates to the host population remaining in an endemic phase. A system will be more resilient with a faster return time since it will be less likely that disturbing effects in year i and then again in year $i + 2$ will induce instability. The speed with which perturbed populations return to the vicinity of an equilibrium is expressed in terms of the largest eigenvalue (λ) of the linearized model by $1/(1 - |\lambda|)$ for $|\lambda| < 1$ (Beddington, Free, and Lawton 1976). With strong parasitoid aggregation ($k = 0.75$), an equilibrium was stable or no equilibrium existed ($\alpha = 1.0$). Nonexistence of an equilibrium was first indicated by Newton's method; however, because this

Table 5. Equilibrium points and eigenvalues of the following parasitoid-host model linearized about these points.

$$H_{t+1} = \delta H_t \exp(-\gamma P_t H_t / (\alpha^2 + H_t^2)) (1 + a P_t / k)^{-k}$$

$$P_{t+1} = H_t (1 - (1 + a P_t / k)^{-k})$$

H is the host density, P is the parasitoid density, P_b is the density of background predators, δ is the rate of increase of H , γ is the maximum number of H consumed per predator, α is the density of H for which predator consumption is $\gamma/2$, (a) is a measure of the parasitoid's searching efficiency with efficiency increasing with larger (a) and K is a measure of the parasitoid's aggregation with respect to host density with low k representing strong aggregation. Values for parameters not given below are: $\delta = 10.0$, $\gamma P_b = 3.75$, $\alpha = 1.0$.

a	Equilibrium Points		Eigenvalues	
	H	P		
<u>k = .75</u>				
3.0	.661	.290	.420 +	.627i
2.5	.734	.295	.509 +	.608i
2.0	.852	.310	.650 +	.580i
1.5	1.120	.399	.907 +	.490i
1.0	*	*		
<u>k = 2.0</u>				
3.0	.558	.283	.371 +	.743i
2.5	.627	.288	.444 +	.705i
2.0	.730	.295	.565 +	.666i
1.5	.918	.323	.780 +	.622i
1.0	1.539	.685	1.166 +	.479i
<u>k = 6.0</u>				
3.0	.513	.277	.365 +	.817i
2.5	.582	.284	.429 +	.763i
2.0	.683	.291	.539 +	.708i
1.5	.859	.311	.742 +	.657i
1.0	1.325	.521	1.117 +	.580i
<u>k = ∞ **</u>				
3.0	.489	.274	.363 +	.886i
2.5	.558	.283	.425 +	.862i
2.0	.659	.290	.529 +	.853i
1.5	.831	.307	.726 +	.870i
1.0	1.256	.475	1.096 +	.856i

* No equilibrium point found

** When $k=\infty$, $(1 + a P_t / k)^{-k} \approx \exp(-a P_t)$ and parasitoid search is random

procedure may not converge to a root of a function, extensive simulations were also employed. The simulations failed to uncover either an equilibrium or a limit cycle. It was also observed that as aggregation increased, the searching efficiency where equilibria ceased to exist became larger (i.e., for $k = 0.5$, no equilibrium could be found for $a = 1.5$).

The eigenvalue analysis of the linearized model provides an initial indication of the stability properties of the system. It is, however, of limited usefulness because it only pertains to the immediate neighborhood about an equilibrium point. Real-world populations are not restricted to "small" changes, and local stability analysis may be quite misleading because parameters may produce local stability; however, the region about the stable point where the model remains stable may be extremely small. In order to determine the global stability properties of (5), simulation was used to outline the boundaries of the host and parasitoid densities for which the system remained stable.

The influence of decreasing parasitoid aggregation on the stability region (i.e., the set of all host and parasitoid densities for which stability is maintained) of the model is portrayed in figure 13. With $k = 0.75$ and $k = 2.0$, the stability region is not closed. This is a result of truncating the analysis at a particular parasitoid density. The region would eventually close with further increases in parasitoid numbers. It is clear that while parasitoid aggregation is not essential, it does improve the system's resilience to perturbation in host or parasitoid numbers. The effect of changes in searching efficiency on the stability region is illustrated for two levels of parasitoid aggregation in figure 14. As with the more simple models, the equilibrium host density increased, though only slightly, with a decline in searching efficiency. More importantly, the stability region became much smaller.

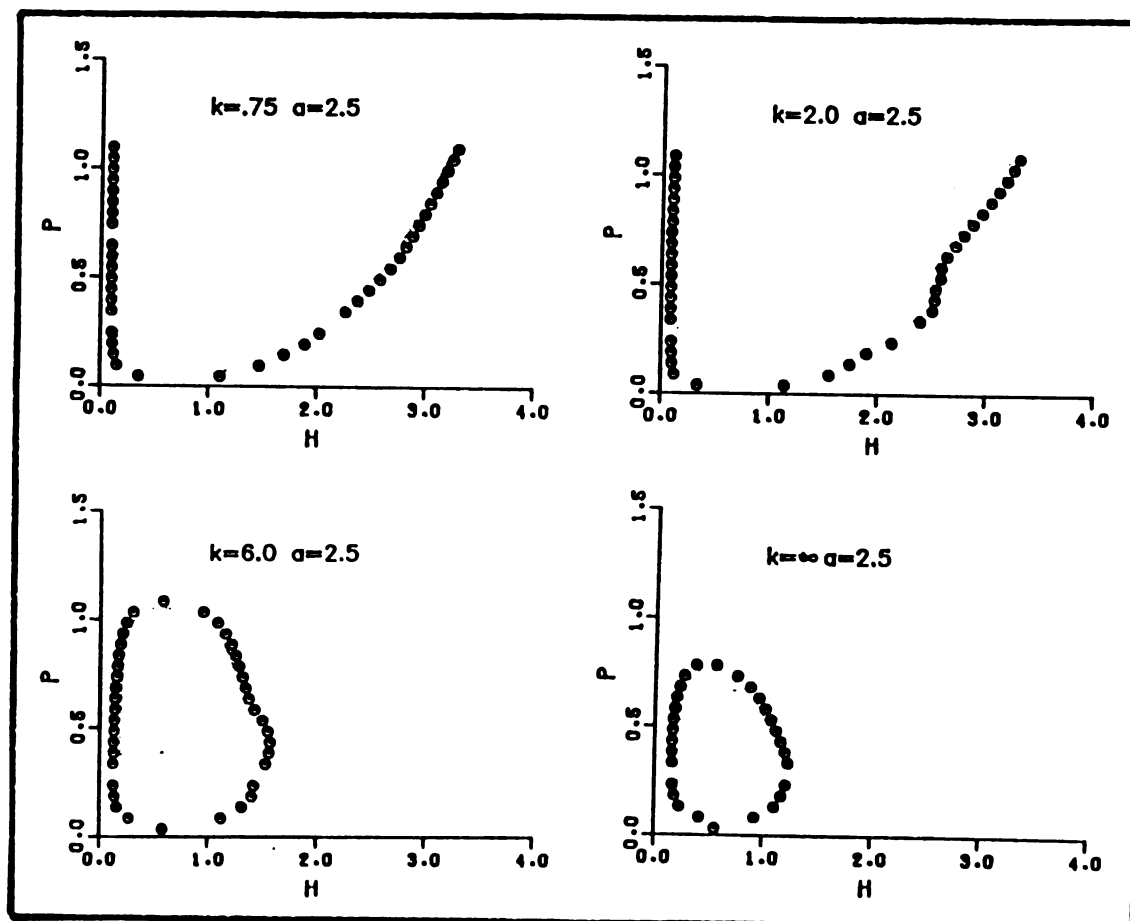


Figure 13. Influence of parasitoid aggregation with respect to host density on the stability region of the following parasitoid-host model:

$$H_{t+1} = H_t \delta \exp(-\gamma P_b H_t / (\alpha^2 + H_t^2)) (1 + a P_t / k)^{-k}$$

$$P_{t+1} = H_t (1 - (1 + a P_t / k)^{-k})$$

The stability region is indicated by the shaded areas. k is a measure of parasitoid aggregation with low k reflecting strong aggregation and (a) is a measure of parasitoid searching efficiency. H is the host density, P is the parasitoid density, P_b is the density of background predators, δ is the rate of increase of H , γ is the maximum number of H consumed per P_b and α is the density of H for which predator consumption is $\gamma/2$. Here, $\gamma P_b = 3.75$, $\alpha = 1.0$ and $\delta = 10.0$.

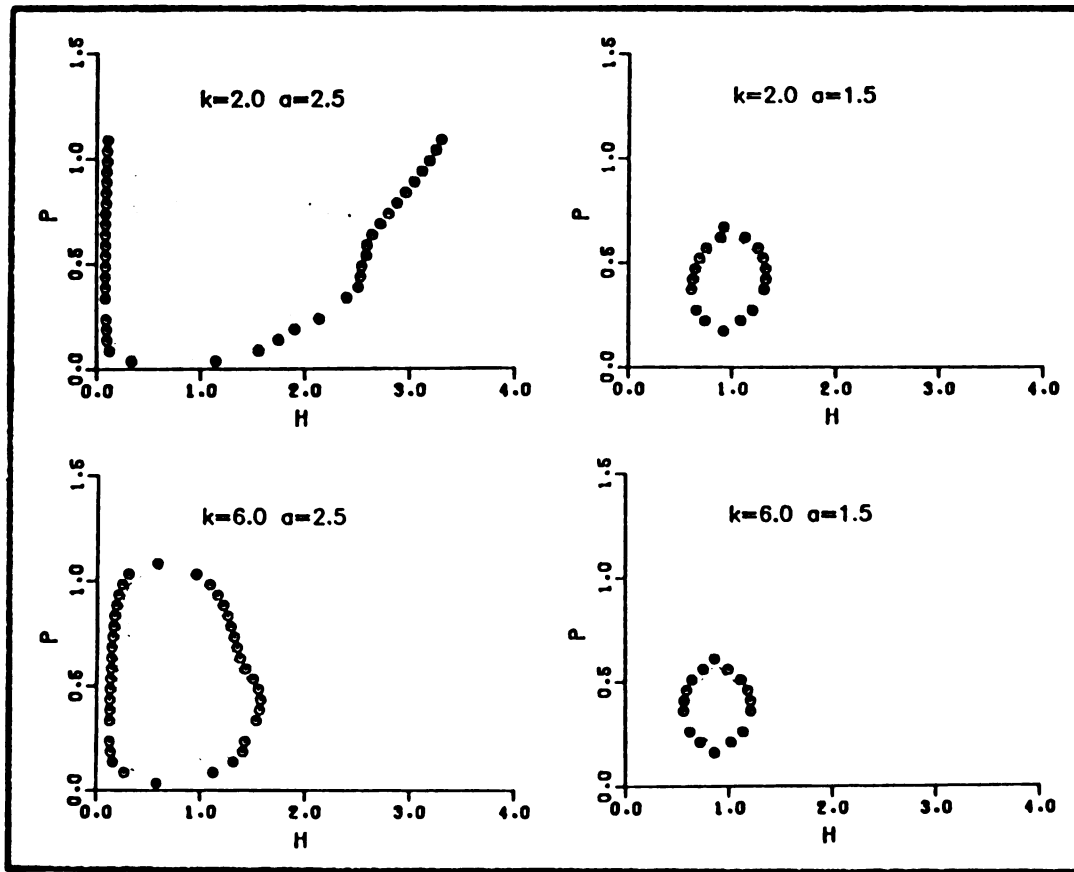


Figure 14. Influence of parasitoid host searching efficiency on the stability region of the following parasitoid-host model:

$$H_{t+1} = H_t \delta \exp(-\gamma P_b H_t / (\alpha^2 + H_t^2)) (1 + a P_t / k)^{-k}$$

$$P_{t+1} = H_t (1 - (1 + a P_t / k)^{-k})$$

The stability region is indicated by the shaded areas. (a) is a measure of parasitoid searching efficiency with lower (a) reflecting poorer efficiency. k is a measure of parasitoid aggregation with respect to host density with low k reflecting strong aggregation. H is the host density, P is the parasitoid density, P_b is the density of background predators, δ is the rate of increase of H , γ is the maximum number of H consumed per P_b and α is the density of H for which predator consumption is $\gamma/2$. Here, $\gamma P_b = 3.75$, $\alpha = 1.0$ and $\delta = 10.0$.

The implications of the empirical observation are far different when viewed in the context of this model as opposed to the simpler one parasitoid-one host models. In this case, in addition to parasitoid aggregation, the attack efficiency of the parasitoid is of paramount importance in establishing a stable and resilient system. This is not a new revelation, since biological control scientists have long emphasized the importance of host searching (Huffaker et al. 1976). Factors which influence the searching efficiency of a parasitoid or group of parasitoids now do not simply determine an equilibrium level but also help determine system stability. As a result, determination of controllable and uncontrollable factors which influence parasitoid-host searching are important aspects of parasitoid management. Aggregation is still a valuable property of a parasitoid from the biological control point of view. However, parasitoids that do not aggregate can still be important natural enemies, and improved pest control can be obtained from management actions taken to improve their searching efficiency.

This is important because empirical data suggests that more times than not, parasitoids fail to significantly aggregate in areas of high host density (Morrison and Strong 1980). These observations may be explained three ways. First, as indicated by our study of G. fumiferanae and studies of other parasitoids, the spatial distribution of these insects is influenced by factors other than host numbers. Second, as discussed by Royama (1970), parasitoids may respond to areas of higher host densities but only in a limited capacity due to a less advanced nervous system. When aggregation is measured in terms of parasitism, slight aggregation will result in constant or declining parasitism when expressed as a function of host density. Finally, these observations may reflect

an inappropriate scale for measuring aggregation since it is well known that the distribution of a population of samples is a function of the size of the sample unit. For instance, G. fumiferanae does not aggregate with respect to the host within a tree but may do so between trees. In passing, we note that this was investigated in our study; however, no relationship was found between host numbers and trap catch in different trees. Further studies of parasitoid behavior, of spatial variation in the distribution of adult parasitoids, and of the spatial variation in parasitism intensity are needed to fully answer the important questions of parasitoid aggregation and thereby determine if aggregation can be manipulated through habitat management.

The results obtained with (5) are not restricted to the particular case examined, since the results will hold for any set of mortality factors which produce a net recruitment curve similar to that portrayed in figure 12. Furthermore, these mortality factors may in themselves produce a stable equilibrium, in which case the parasitoid serves to enlarge the stability region about an equilibrium. The inclusion of a limited capacity for parasitism by each parasitoid so that the number of hosts parasitized does not increase indefinitely as the number of hosts increases will not alter the general results obtained. The affect of inclusion of this limitation will be a contraction of the stability region, the size of which will be dependent on the density at which limitation occurs.

Conclusions

In this paper, we have presented data which indicate that: (1) the searching efficiency of G. fumiferanae is reduced in wet and cool weather, (2) habitat does not influence the parasitoids' ability to obtain nutrients and moisture, and (3) the spatial distribution of the adult female parasitoid and of

the ovipositions made by these insects within a tree crown is influenced by temperature and light. These results and those obtained by a number of other authors point to the fact that abiotic factors and biotic factors other than the host play an important role in determining the number and distribution of hosts attacked by a parasitoid. This, in turn, may have a pronounced affect on the ability of a parasitoid to act as a biological control agent. In some cases, the factors which influence the intensity and distribution of the parasitoids' searching activity will be amenable to manipulation and should then serve as an object of control for parasitoid management. However, identification of these factors requires detailed studies of the temporal and spatial dynamics of the adult parasitoids.

Forest Harvesting and the Spruce Budworm

Introduction

The eastern spruce budworm is native to North America and is distributed throughout the northern boreal forest from Alberta to Maine and the Maritimes. The preferred hosts are balsam fir (Abies balsamea (L.) Mill.), white spruce (Picea glauca (Muench) Voss), red spruce (P. rubens Sarg.), and to a lesser extent, black spruce (P. mariana (Mill.) B.S.P.) (Greenbank 1963). Defoliation of balsam fir and spruce by spruce budworm occurs at periodic intervals. Depending upon defoliation intensity, the death of individual trees or whole stands can occur. Spruce and fir are valued for paper production and lumber. Budworm outbreaks often kill more trees than can be used rapidly. In addition, a future shortage of fiber can result from extensive budworm-induced tree mortality.

Outbreaks of the budworm occur at 20 to 40 year intervals. The outbreaks themselves may extend only 8-10 years, but the effects are longer lasting. In the past, especially in the East, large-scale spraying programs minimized the budworm damage. However, concerns have been voiced about the effectiveness and environmental impact of the spray programs. In the Lake States, recent supplies of spruce and fir have exceeded demand. As a result, few aerial sprayings of forests were conducted. Instead, greater emphasis was placed on cutting to salvage damaged material or to presalvage stands.

Management techniques are needed that take demand for fiber into account, take commercial management objectives into account, and provide resistance to spruce budworm. Without such management techniques, the future will hold the same scenario that has developed during recent budworm outbreaks; a large acreage of killed timber with no hope of marketing all of the product.

There are several techniques that can be used. These techniques can be grouped into three general approaches: (1) those which are directed at the forest, (2) those which are directed at the insect, and (3) those which combine (1) and (2).

GROUP I.

The first group of approaches, those directed at the forest, largely involve the way the forest is harvested or the timing of harvest. The following illustrate what is meant:

1) No Action — This is the deliberate avoidance of any action by man. This approach is appropriate where the cost of utilizing a particular stand is greater than the value of the product it will yield. Stands categorized as beyond salvage fall into this category.

2) Salvage — This is the marking, selling, and harvesting of stands which are in the process of dying but have not deteriorated too far to be uneconomical to cut. The prime limitations of this tactic are lack of manpower to carry out the action and lack of spruce-fir markets where loggers can sell the pulpwood. During a spruce budworm outbreak, an oversupply of material results in both of the above.

3) Presalvage — This is the marking, selling, and harvesting of stands which are healthy but vulnerable to spruce budworm (i.e., these stands, because of age and composition, would suffer damage if subjected to budworm outbreak). Presalvage is difficult to carry out efficiently and effectively during an outbreak because both manpower availability and market availability are limiting.

4) Changing Stand Composition — This involves the outright removal of some spruce and fir from stands to encourage a species mix. Although an elegant concept, realization of such conditions over a large area is unrealistic.

5) 40-year Rotation — This is the deliberate utilization and marketing of stands such that no individual stand ever exceeds 40 years of age. This is based on the supposition that spruce budworm creates the greatest damage in older stands (usually older than 50 years of age). In concept, this approach is perhaps the most appealing of all techniques available today. However, it is too idealistic. Many spruce-fir stands already exceed 40 years of age. In the next rotation, this is a target that forest managers may be able to aim toward.

GROUP II.

The second group of techniques are activities directed at the spruce budworm itself and, for the most part, involve chemical and biological pesticides. These techniques are often inappropriate. The prime reason is that techniques directed at the insect are often uneconomical for stands being managed for timber production.

GROUP III.

The third group of techniques are those which are combinations of methods directed at the forest and at the insect. By this we mean that through forest directed activities we affect factors which influence spruce budworm numbers. This group of techniques relies on small block cutting which adds a "checker-board" pattern to existing healthy stands (those which we expect to hold for 5 to 20 years and then market). These techniques are explicitly designed to add resistance to residual stands through cutting by enhancing predator and parasite populations and increasing mortality that occurs during the larval dispersal period.

A project was begun in 1979 to examine how the problem of budworm, mature forests, and the demand for wood fiber could be addressed by partial

harvesting of existing, living stands. The following is a report of work done during this project. It is comprised of three parts: (1) a theoretical basis for partial cutting, (2) the economic aspects of the strategy, and (3) a measurement of the response of the biological system to partial cuts.

A Theoretical Basis for a Strategy of Partial Cuts

Fluctuations in spruce budworm numbers have been the focus of scientific study for several decades. It has been suggested that population changes can be described by a model whose general form has been used for many different biological populations ranging from bacteria to big game (e.g.; Noy-Meir 1975, Gulland 1975, Clark and Mangell 1979, Petermen et al. 1979, Weckham and Botsford 1980, Fleming 1980, Campbell and Sloan 1977, Clark et al. 1979, McLeod 1979, Southwood and Cummins 1976, Ludwig et al. 1978). The components of such a model include an intrinsic logistic growth rate coupled with mortality factors that increase in intensity as the population density increases (density-dependent). The growth rate and density-dependent mortality factors are also often coupled to habitat conditions.

With such models, it is possible to analyze population changes over a range of densities from very low (endemic) to very high (epidemic). When this is done, analysis often reveals conditions where the rate of increase is balanced by an equal mortality rate. Such conditions are termed equilibrium states. If a population tends to remain at an equilibrium, it is considered stable. In the case of the spruce budworm, two stable equilibrium states may be evident: one at very low densities and one at very high densities.

The rate of change of the budworm population as a function of budworm density is portrayed in figure 15. In this figure, the solid line depicts the intrinsic biological growth rate of the budworm population. The dashed lines are losses due to predation and parasitism (M). Where the dashed line lies above the solid line, the net growth rate of the budworm population is negative, and where the dashed line lies below the solid line the net growth rate is positive. Points of intersection of the dashed and solid lines indicate possible equilibrium points. For an intermediate value of M , there are stable low and high density equilibrium points (A and C) and an unstable intermediate equilibrium point (D). Budworm numbers will remain low provided their density remains below T. If they exceed T, the population density will move to C.

The forest plays an important role in determining fluctuations in budworm numbers. This role is manifested through the influence of forest composition and forest structure on the intrinsic growth rate of the budworm population and on the level of budworm predation and parasitism.

Forest composition and structure influence the intrinsic growth rate of the budworm population through egg mortality from parasitism and through the dispersal loss of early instars. Typically, the intrinsic growth rate of an insect population is determined by the number of eggs laid by females. However, with budworm, most significant density-dependent mortality occurs after the budworm are established in feeding sites in the spring. Hence, the number of surviving third instars represents the intrinsic growth rate for a particular year.

Parasitism of budworm eggs has been found to increase with an increasing proportion of non-host trees in a stand (Kemp and Simmons 1979a). Unfortunate-

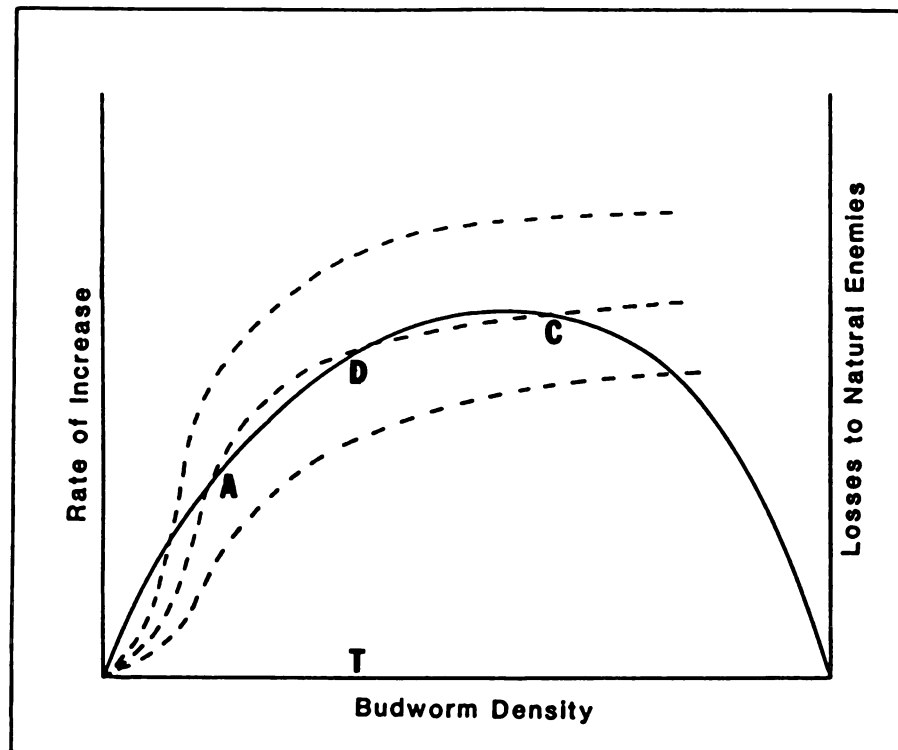


Figure 15. The relationship between the rate of increase of spruce budworm populations (solid line) and different levels of predation and parasitism (dashed lines)

ly, little is known of egg parasitism at low budworm densities. At high densities, it is an insignificant mortality factor.

Dispersal loss of budworm larvae occurs in the fall and spring and results in a 60% to 85% reduction in the population (Miller 1958, 1975). Mortality factors during the dispersal period are: (1) air dispersal to non-host material, (2) predation, (3) failure to spin hibernaculae, and (4) diapause-free development (Miller 1958). Of these, the most important is air dispersal to non-host material. Kemp and Simmons (1979b) found that a higher proportion of non-host trees in the understory, reduced crown closure, and the presence of aspen in the overstory resulted in higher mortality during the dispersal period. Similar results were obtained in a simulation study of spruce budworm dispersal (Kemp et al. 1980). A recent report on the closely related jack pine budworm (Choristoneura pinus) (Freeman) indicated that dispersal losses increased with decreased stand stocking (Batzner and Jennings 1980).

The picture painted is that, in stands with non-host trees and open areas, the intrinsic rate of increase of the budworm is reduced. As a forest stand matures and crown closure increases, the growth rate of the budworm population increases. Depending on the magnitude of the increase in the growth rate of the budworm population, the change in early larval survival may be sufficient to catalyze a budworm outbreak. However, forest dynamics also have a significant effect on natural control agents. The most important of these natural enemies are those which attack the large larvae and pupae.

Stand composition and structure can influence the mortality of large larvae and pupae through bird predation. Views on the importance of bird predation in maintaining budworm populations at low numbers are varied. We feel that it is

unlikely that bird predation alone is responsible for maintaining budworm at low densities. However, when complemented with other mortality factors, bird predation is important.

The bird predator guild can be classified into two groups: ground feeders and crown feeders. Gage et al. (1970) have shown that ground feeders feed less frequently on budworm than crown feeders, while their mean consumption per individual is much higher. If we assume that differences in feeding frequency and consumption rates tend to cancel each other, then the important aspect of the bird predator guild is not the species mix, but rather the density of all bird predators. Data presented by Titterington et al. (1979) and Gage and Miller (1978) suggest that the densities of the predator guild reach a maximum in stands characterized by a mix of hardwoods, softwoods, and stand openings. As a stand matures, crown closure increases, tree species diversity declines, and the number of avian predators decreases.

In addition to changes in bird predator numbers, forest dynamics may also influence the searching efficiency of bird predators. Birds search foliage in order to find budworm. As the forest matures, the foliage area to be searched increases and the efficiency of birds in locating and capturing budworm likely declines.

A large numbers of parasitoids attack the late instars and pupae of spruce budworm. The role of these parasitoids as mortality agents has been largely discounted since they depend on alternate hosts and their parasitism rates are generally low. However, no study has attempted to determine their influence on budworm dynamics at low densities. Stand characteristics influence the parasitism of budworm by these parasitoids. Simmons et al. (1975) found that pupal

parasitism of budworm increased as stand diversity increased and crown closure decreased. The reasons for this are twofold: (1) increased stand diversity provides more habitat for alternate hosts required by the pupal parasitoids, and (2) stand openings provide sources of food and water for the adult parasitoids.

The net effect of forest-induced changes on avian predators and insect parasitoids is a reduction in their ability to limit budworm numbers as the forest becomes more uniform in composition and as open area declines.

The contentions raised here are supported elsewhere. In particular, it has been found that budworm-induced tree mortality is related to stand composition and often declines with increases in the density of non-host trees and along borders of stand openings (MacLean 1980).

It is clear that the dynamics of the spruce-fir forest and the budworm are closely related. In general, as a forest matures, the food resources of the budworm increase and the impact of various mortality factors acting on the budworm are diminished. Forest management might therefore make an effort to reduce the impact of budworm by either maintaining or transforming the forest to a successional state where these mortality factors can better limit budworm numbers. Such a state may be achieved through the use of partial cuts.

Mathematical Analysis

A theoretical basis for partial cutting to reduce budworm impact has been presented. In essence, a system (the forest, the budworm, and a harvesting strategy) has been envisioned through which a set of objectives (minimizing fiber loss, maintaining a steady supply of fiber, or maximizing economic returns) might be met. The next step is to analyze this system through the use of a

mathematical model. In so doing, we hope to increase understanding of real world phenomena and better develop management or design policies.

If, instead of seeking better ways to manage spruce fir stands, we were asked to design a controller for an industrial chemical process, the task would be relatively straightforward. Mathematical models could be employed to design the controller and analyze its operation. However, mathematical models of biological processes are usually too abstract to capture the real world. For this reason, they normally cannot be used alone as a design tool. Instead, they should be used to explore a range of possible outcomes, and then one or some of the logical management approaches can be field tested. This is the philosophy adopted here.

As stated earlier, the swift change that can occur in budworm numbers depends in part on slow changes in forest composition and forest structure. In order to capture the complete dynamics of the spruce budworm and spruce fir forest, these fast and slow changes must be coupled. However, we are not interested in the dynamics of the budworm from the beginning of one outbreak to the next one, but rather in the transition from the endemic to the epidemic states. This is because our objective is to prevent, delay, or lessen the severity of a budworm outbreak in the residual forest stand following a partial cut.

The rate of change in budworm numbers for a particular forest condition is given by the intrinsic rate of increase of the budworm population (feeding third instars) minus the rate at which budworm are lost to mortality factors. This rate can be described in terms of a mathematical model:

$$\frac{dB}{dt} = rBs - (B^2/(\alpha^2 + B^2))\delta \quad (1)$$

In (1), B is the budworm density per m^2 foliage, r is the rate of increase of the budworm, S is the number of m^2 units of foliage per hectare, α is the density per m^2 foliage of budworm at which one half the maximum efficiency of budworm natural enemies is reached, and δ is the maximum number of budworm per hectare lost to natural enemies. A differential equation is an approximation of what is actually a discrete time process. However, adoption of a continuous representation facilitates analysis and will not invalidate any general conclusions reached.

Ludwig, Jones, and Holling (1978) used a form of (1) and concluded that δ is principally attributable to bird predation. To begin, we will adopt their conclusions and use their estimates of parameters of (1) which place the budworm population in a transition between the endemic and outbreak states. Equation (1) can then be written as:

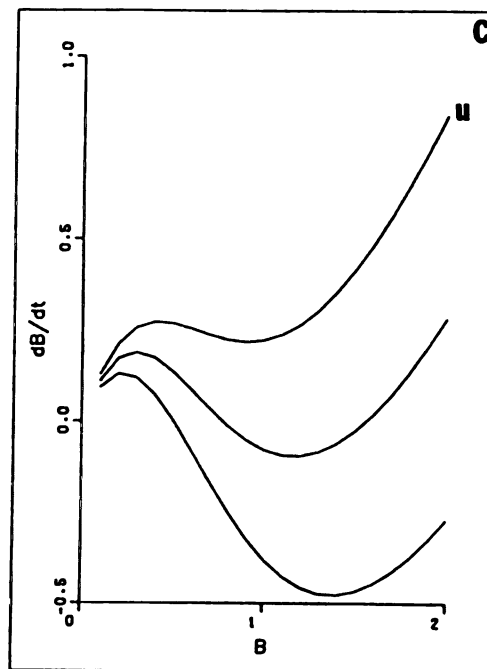
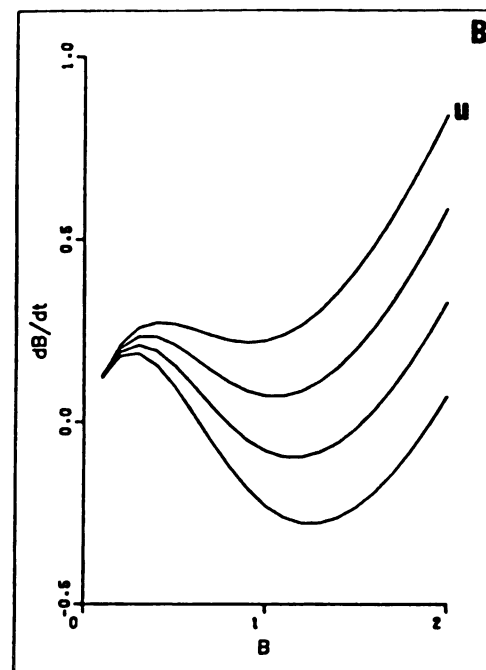
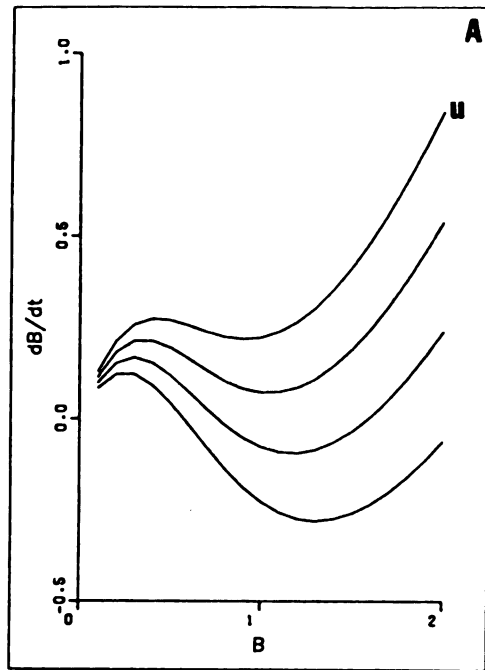
$$dB/dt = 1.52(B)37050 - (B^2(1.1^2 + B^2))106210$$

The relationship between the rate of increase of the budworm population and the budworm density for these values is presented as curve u in figure 16. It can be seen that the rate of change of the budworm is greater than zero for all budworm densities, and budworm numbers will therefore quickly increase. The effect of reducing the rate of increase by 10%, 20%, and 30% is portrayed in figure 16. With a 20% and 30% reduction of the intrinsic rate of increase, an outbreak would not develop unless budworm numbers exceeded 1.5 and 2 larvae per m^2 , respectively. The reduction in this rate may be brought about as a result of increased dispersal loss in areas subjected to a partial harvesting strategy.

Figure 16. The influence of different levels of dispersal loss and predation on the rate of change of spruce budworm numbers. This rate is described by;

$$dB/dt = rBS - (B^2/(\alpha^2+B^2))\delta$$

B is the number of budworm per m² foliage, r (1.52) is the growth rate of B, S (37050) is the number of m² units of foliage per hectare, α (1.1) is the density of budworm at which predation is 1/2 the maximum and δ (106210) is the maximum predation of budworm per hectare. The topmost curve in A, B and C correspond to these values. In A, dispersal loss is increased 10, 20 and 30%; in B predation is increased 10, 19 and 26%; and in C both dispersal loss and predation are increased 10 and 10% and 20 and 19% respectively.



In addition to a reduction in the intrinsic rate of increase, a partial cutting strategy will also result in an increase in losses to natural enemies. If these losses are wholly attributable to bird predation, this comes about as a result of an increase in bird densities and a decrease in foliage area.

The effect of increasing losses to natural enemies by 10%, 19%, and 26% is illustrated in figure 16 . Once again, an outbreak will not develop unless the critical thresholds of budworm densities are exceeded.

By combining the influence of partial harvesting on the intrinsic rate of increase and on the loss to natural enemies, dramatic changes in the rate of increase of the budworm population can be achieved. This is illustrated in figure 16 for a 10% reduction in the rate of increase and 10% increase in losses to natural enemies, and a 20% reduction in the rate of increase and a 19% increase in losses to natural enemies, respectively. In the latter case, the threshold density for an outbreak is approximately 2.5 budworm per m^2 .

Unfortunately, the analysis presented cannot be considered conclusive. While the general forms of the relationships presented are likely correct, questions exist with respect to model components and the actual parameters used. First, it is unlikely that avian predators are the only density-dependent mortality factors. The influence of parasitic insects and infectious diseases has been ignored. Second, the maximum consumption rate of the avian predators is a gross estimate and may deviate by $\pm 30\%$. Finally, it is not possible to predict the actual effect of a partial cut on the intrinsic rate of increase or on losses to natural enemies. The important point, though, is that modest changes in the intrinsic rate of increase of the budworm and in the number of budworm lost to

natural enemies can have significant effects on the rate of increase of the budworm population.

An obvious confounding factor is the immigration of budworm into stands which have been partially cut. This immigration need not be extraordinary to push budworm densities beyond the threshold of 2 to 5 larvae per m^2 foliage for which budworm numbers cannot be regulated by natural enemies. Miller et al. (1978) estimated that moths immigrating into a test plot from surrounding areas with moderate to high budworm densities deposited ca. 10 egg masses per m^2 foliage. Assuming 20 eggs per mass and 80% cumulative mortality of eggs and small larvae, the density of large larvae will exceed the mortality caused by (functional response) natural enemies. For this reason, a partial harvest may not be able to prevent high budworm densities in treated stands.

Within the context of the model, once the rate of increase of the budworm population exceeds natural enemy induced mortality, the population quickly increases to the carrying capacity of the habitat and remains there until the food supply is exhausted. However, there are instances in which the budworm population has increased well beyond an endemic density but did not destroy the habitat. This model, therefore, cannot be considered representative of all real world situations. It is conceivable that, by decreasing the intrinsic rate of increase of the budworm and increasing losses to natural enemies, an outbreak may not be prevented but may be diminished in intensity. As a result it is important to examine the dynamic interaction between the budworm and forest when budworm numbers are greater than endemic levels.

Ludwig et al. (1978) suggested using two variables to describe the forest: the number of units of an area of foliage (S), and an artificial variable to

describe the physiological state of the trees (E). In this case, S is the number of m^2 units of foliage per hectare. The rate of change of these variables is described by the following model:

$$dS/dt = r_s S(1 - (SK_s)(K_E/E)) \quad (2)$$

$$dE/dt = r_E E(1 - (E/K_E)) - P(B/S) \quad (3)$$

In (2), the increase in S is limited by a maximum (K_s) which we have set equal to 49,400 per hectare. A similar situation exists for E; however, the peak physiological condition (K_E) is equal to 1. Where the physiological condition of the tree is poor, the value of S/K_s is multiplied by K_E/E so that S does not increase. In (3), B/S is budworm larvae per m^2 foliage and P is the rate of consumption of foliage per larvae. It is assumed that a decline in the physiological condition of the tree is directly proportional to the loss in foliage. S does not decline directly as a result of budworm feeding, but rather through a decline in the physiological well-being of the tree. Ludwig, et al. estimated P as 1.5×10^{-3} , r_s as .10 and r_e as 1.0. We will use these values initially.

For a given budworm density, (2) and (3) constitute a dynamic system which has no analytical solution. In order to gain insight into the properties of this system, graphical methods are used. In figure 17, the values of S and E for which the rates of change of each is zero are plotted.

The points where these lines intersect are equilibrium points. For any initial value of S and E and a given value of B, the rate of change of the complete system (dS/dE) can be evaluated. By so doing, the dynamics of S and E can be determined. Approximate system trajectories for various values of S and E are given in figure 17. If the equilibrium points exist, then the forest will remain alive, providing the physiological condition of the trees is good.

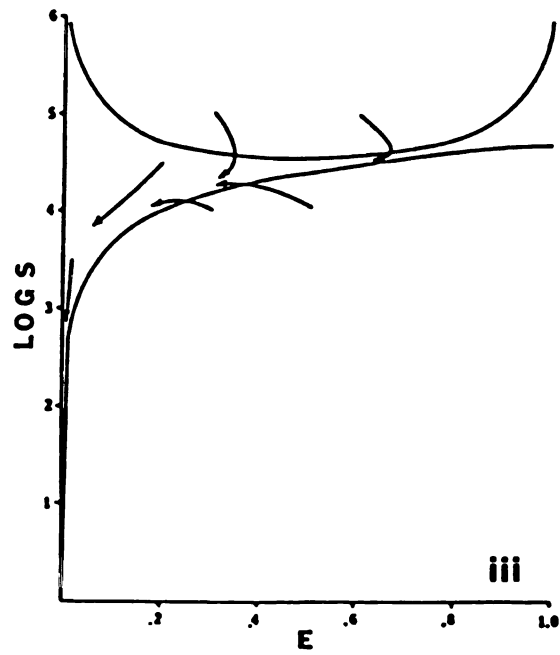
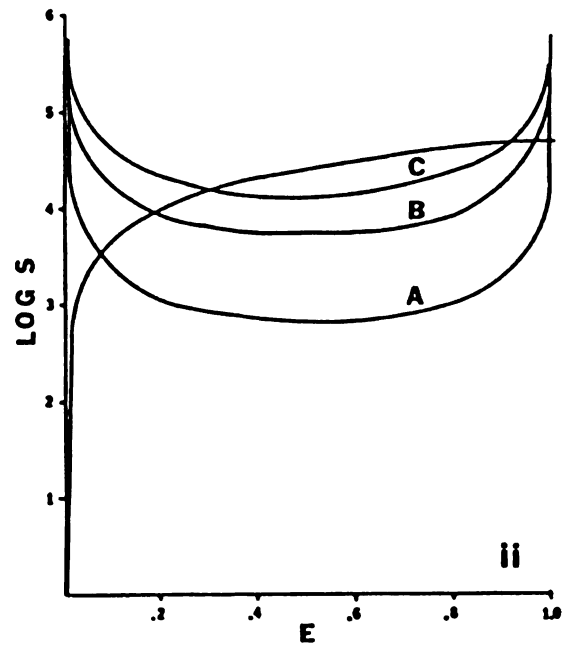
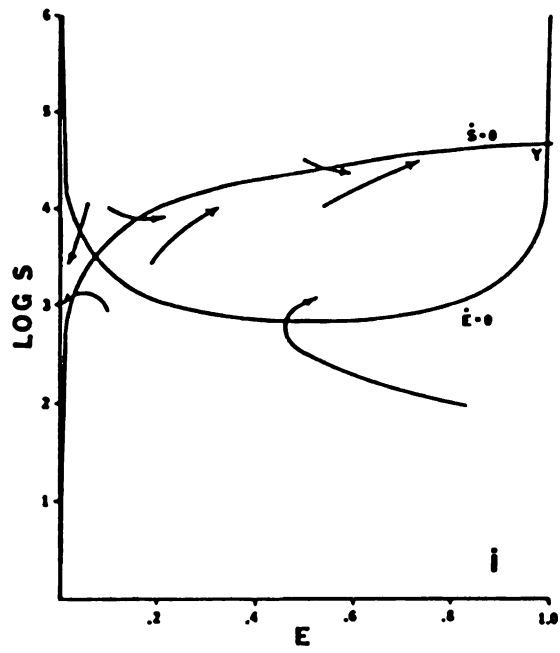
Figure 17. The influence of spruce budworm defoliation on the survival of host trees. The dynamics of the host trees is described by two equations¹;

$$dS/dt = r_S S(1 - (S/K_S)(K_E/E))$$

$$dE/dt = r_E E(1 - (E/K_E)) - P(B/S)$$

Where S is the number of m^2 units of foliage per hectare, r_S (.1) is the growth rate of S , K_S (49,400) is the maximum S per hectare, E is the physiological condition of the tree, K_E (1.0) is the maximum E , r_E (1.0) is the growth rate of E , P (.0017) is the proportion of a m^2 unit of foliage consumed by 1 budworm and B is the number of budworm per hectare. In (i) $B = 1 \times 10^5$. The arrows indicate general system dynamics for various initial conditions. In (ii) $B = 1 \times 10^5$ for A, 8×10^5 for B, and 2×10^6 for C. In (iii) $B = 5 \times 10^6$ and extensive tree mortality occurs.

¹Ludwig, D., D.D. Jones, and C.S. Holling. 1978. Qualitative analysis of insect outbreak systems: The spruce budworm and forest. J. Anim. Ecol. 47:315-332.



The forest (S) will succumb to budworm under two conditions. First, the equilibrium points may vanish. This will occur if budworm densities exceed some critical level. Second, the physiological state of the trees may decline below a critical value as a result of budworm feeding.

The second condition can also be evaluated graphically. In figure 18, equation (3) is portrayed for different values of B/S and r_E . As shown, the tree remains vigorous even for relatively high densities of budworm and values of r_E less than that given by Ludwig et al. In the real world, it is likely that sustained moderate defoliation will result in a decline in r_E , and the physiological condition of the tree may then decline. In addition, parameter values used are gross estimates and will vary from site to site. Accurate predictions of the budworm density required to cause extensive tree mortality cannot be made. However, this is not the purpose of the analysis. The important point is that extensive tree mortality will not occur with moderate budworm densities for a number of years. Hence, if a policy of partial harvesting can lessen the intensity of an outbreak in the residual stand, mortality of the remaining trees can at least be delayed and may be reduced.

To conclude this section we have shown that a reduction in the rate of increase of budworm populations coupled with an increased loss of budworm to natural enemies dramatically alters the dynamics of the insect. Immigration of moths from surrounding stands may, however, cancel these effects. The forest can tolerate moderate defoliation by the budworm for many years. It is conceivable that, as a result of a partial cut, the intensity of an outbreak is diminished. Without more information, though, a mathematical analysis can go no further. A real world evaluation of a partial harvest policy is desirable and

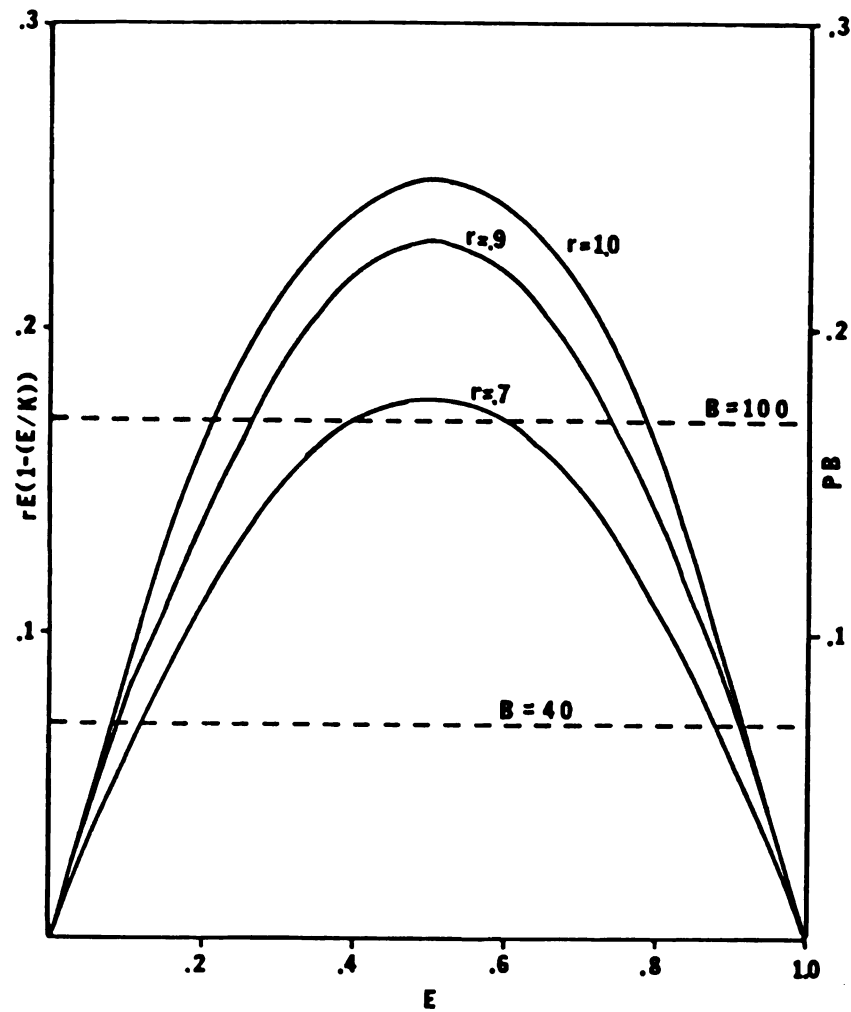


Figure 18. Influence of spruce budworm on the physiological condition of host trees. The physiological condition is described by¹

$$dE/dt = rE(1-(E/K)) - PB$$

where E is the physiological condition, r is the rate of increase of E , K (1.0) is the maximum E , P (.0017) is the rate of consumption of a m^2 unit of foliage per larvae and B is the budworm density per m^2 foliage. The dashed lines are PB and the solid lines are $rE(1-(E/K))$.

¹Ludwig, D., D.D. Jones, and C.S. Holling. 1978. Qualitative analysis of insect outbreak systems: The spruce budworm and forest. *J. Anim. Ecol.* 47:315-332.

necessary but also difficult to conduct. Nevertheless, an effort has been made to perform such an analysis.

Implementation and Assessment of a Partial Cut Strategy

A policy of partial harvesting was evaluated on three sites in the Hiawatha National Forest in Delta County in Michigan's Upper Peninsula. The specific sites are all within 30 miles of the city of Escanaba. The spruce-fir type is scattered throughout the region, with individual stands ranging from about 30 acres up to about 100 acres in size.

Three forest stands (fig. 1) were selected for implementing the partial harvest strategy based on the following criteria: (1) species composition: spruce fir type with some hardwood component, either aspen or northern hardwoods; (2) area size: a minimum of 40 acres with a control plot of no less than 10 acres, preferably adjacent to the treatment plot; (3) budworm density: low budworm numbers at the time of harvesting; and (4) harvestability: sufficient volume of timber so that partial cutting may be commercially feasible, if road-building costs and distance to mills is not prohibitive. In fall 1979, stands 1 and 3 (fig. 1) were identified. In fall 1980, stand 2 (fig. 1) was added, although budworm densities were already at moderate population levels.

In stand 1, cuts laid out as patches were used to partially harvest the stand. The layout of the cuts and the control plot is shown in figure 19. Harvesting was conducted in the winter of 1979/1980. In stand 2, cuts were laid out in strips and were made during the winter of 1981. Harvested strips are 40 m wide and the uncut strips are 60 m wide. The layout of the strips and the control plot is shown in figure 19. In stand 3, cuts were laid out in strips 20 m wide with an uncut

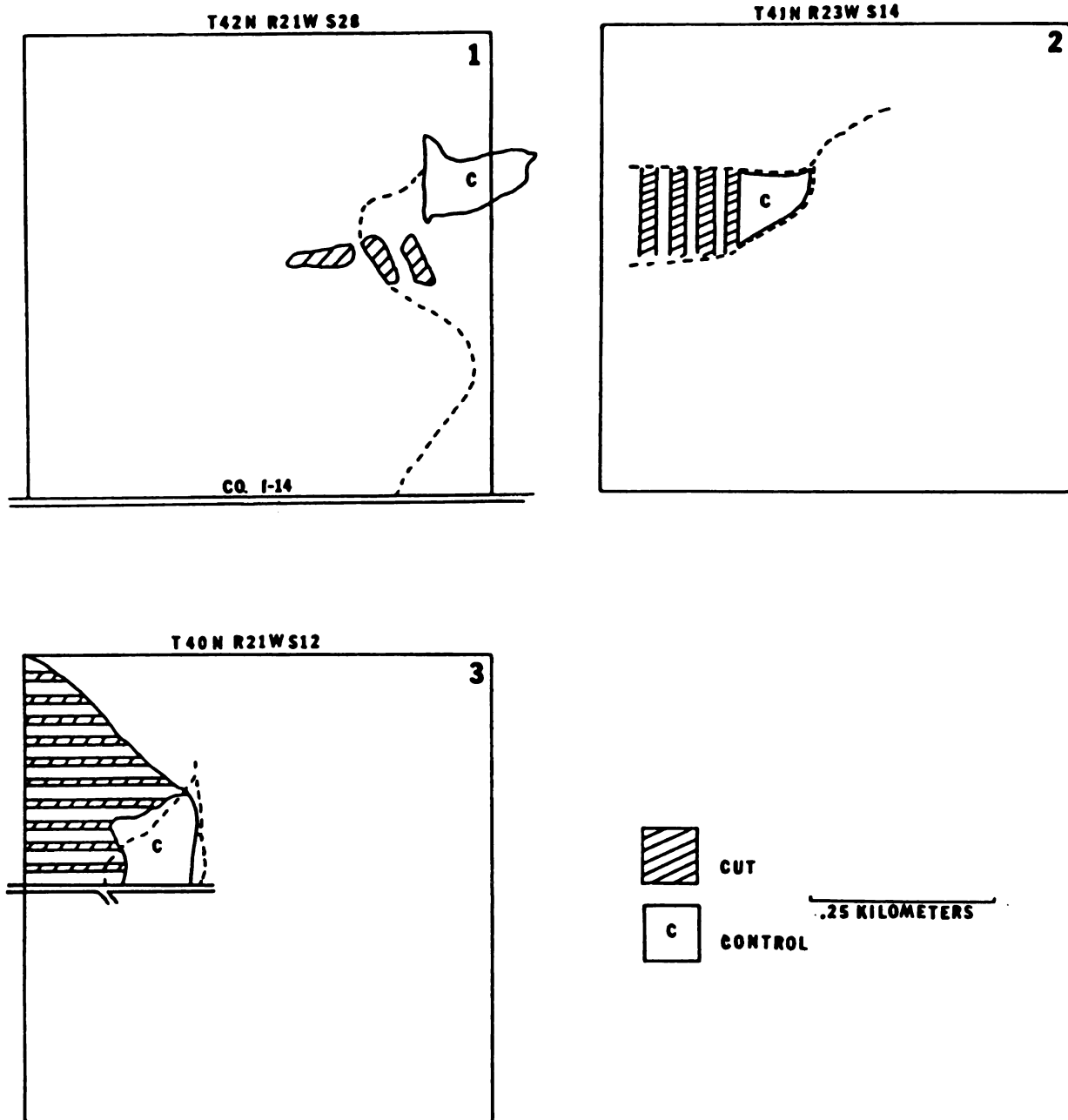


Figure 19. Layout of cut and control areas in stands 1, 2 and 3.

strip 40 m wide separating each cut (fig. 19). Harvesting of this area took place in the winter of 1979/1980.

The structure and composition of each cut and control area was described by measuring stand parameters in five fixed-radius plots in the residual stand of the treatment areas and in the control areas. In the strip cuts, plots were established in the center of each residual strip. In the patch cut, plots were located 20 m from the edge of the cut. In all control areas, plots were located 60 m or more away from a cut area.

Plot measurements were made according to procedures developed by Mog and Witter (1979). This data is presented in tables 6 through 8. The live tree species composition and tree condition parameters for budworm hosts in the cut and control areas for stands 1 and 2 are very similar. In stand 3, the total percentage of budworm hosts is approximately the same; however, the control area has a larger percentage of white spruce.

Evaluation of a policy for managing or designing a system must address two things: (1) Is the policy feasible and (2) are the objectives as originally set forth met by applying the policy? The feasibility of partial harvesting is determined by profitability and compatibility with other forest management objectives. Whether partial cutting can help meet these objectives is determined by how this policy affects the budworm population.

Feasibility of a Policy of Partial Harvests

Any feasibility analysis of a partial cut strategy is based on determining when and how much of a forest stand to harvest. The timing of timber harvest involves two considerations: (1) stand growth, and (2) financial maturity of a

Table 6. Comparison of species composition of live trees and tree condition parameters for spruce budworm host trees by treatment in stand 1. Species composition is based on data collected from 5 .04 hectare plots and tree parameters are based on data from 5 .02 hectare plots.

	Cut				Control			
	<u>Trees</u> hectare	Σ	<u>Basal₂</u> area m hectare	Σ	<u>Trees</u> hectare	Σ	<u>Basal₂</u> area m hectare	Σ
Balsam fir	554	58	12.6	40	563	53	13.7	39
White spruce	20	2	1.2	4	25	2	1.7	5
Trembling aspen ¹	198	21	12.1	39	237	22	12.3	35
Paper birch	44	4	1.0	3	124	12	2.9	8
N. white cedar	114	12	3.1	10	89	8	3.7	10
Sugar, red maple	5	1	0.2	1	20	2	0.4	1
Other hardwoods	15	2	0.8	3	10	1	0.2	1
Hemlock	0	0	0	0	5	0	0.4	1
All species	950	100	31.0	100	1073	100	35.3	100
Parameter	$\bar{x}$		$s_{\bar{x}}$	n	$\bar{x}$		$s_{\bar{x}}$	n
Balsam fir								
DBH (cm)	17.5		0.69	53	15.9		0.42	62
Tree height (m)	14.8		0.41	53	14.5		0.34	62
Crown position ²	2.7		0.15	53	2.8		0.10	62
Live crown length (m)	7.2		0.37	53	8.0		0.36	62
Dead crown length (m)	1.0		0.15	53	1.7		0.15	62
Proportion ₃ trees dead	0.11		0.04	53	0.17		0.05	62
site index	60.0			29	60.0			27
White spruce								
DBH (cm)	32.6		3.46	3	26.4		4.25	4
Tree height (m)	18.0		1.56	3	17.8		1.85	4
Crown position ²	1.0		0.0	3	2.2		0.5	4
Live crown length (m)	10.5		1.79	3	8.8		0.95	4
Dead crown ₃ length (m)	3.7		0.0	3	4.0		0.0	4
site index	52.0			12	55.0			13

¹Includes balsam poplar

²Crown position ranking: 1-dominant, 2-co-dominant, 3-intermediate, 4-suppressed

³Based on USDA Forest Service Lake States Exp. Sta. Tech. Notes 465 and 474 by S. R. Gevorkiantz

Table 7. Comparison of species composition of live trees and tree condition parameters for spruce budworm host trees by treatment in stand 2. Species composition is based on data collected from 5 .04 hectare plots and tree parameters are based on data from 5 .02 hectare plots.

Species	Cut				Control			
	<u>Trees</u> hectare	Σ	<u>Basal₂</u> <u>area m</u> hectare	Σ	<u>Trees</u> hectare	Σ	<u>Basal₂</u> <u>area m</u> hectare	Σ
Balsam fir	763	71	18.12	66	788	85	16.29	79
White spruce	0	0	0	0	6	1	0.07	1
Aspen	313	29	9.18	34	131	14	4.36	20
Total	1076	100	27.30	100	925	100	20.72	100
Parameter	$\bar{x}$		s^2_x	n	$\bar{x}$		s^2_x	n
Balsam fir								
DBH (cm)	16.85		0.51	54	15.70		0.41	53
Tree height (m) ₁	14.66		0.30	54	14.09		0.37	53
Crown position ₁	2.40		0.12	54	2.72		0.16	53
Live crown length (m)	7.78		0.33	54	6.03		0.28	53
Dead crown length (m)	.50		0.16	54	0.35		0.14	53
Proportion ₂ trees dead	0.16		0.05	54	0.19		0.05	53
site index ₂	62			12	65			12

¹Crown position rankings: 1-dominant, 2-co-dominant, 3-intermediate, 4-suppressed

²Based on USDA Forest Service Lake States Exp. Sta. Tech. Notes 465 and 474 by S. R. Gevorkiantz

Table 8. Comparison of species composition of live trees and tree condition parameters for spruce budworm host trees by treatment in stand 3. Species composition is based on data collected from 5 .04 hectare plots and tree parameters are based on data from 5 .02 hectare plots.

	Cut				Control			
	<u>Trees</u> hectare	%	<u>Basal₂</u> <u>area m</u> hectare	%	<u>Trees</u> hectare	%	<u>Basal₂</u> <u>area m</u> hectare	%
Balsam fir	469	55	12.3	39	183	29	5.4	16
White spruce	35	4	1.3	4	247	27	7.4	21
Trembling aspen ¹	193	23	13.5	43	114	12	11.0	31
Paper birch	84	10	2.3	7	247	27	6.3	18
N. white cedar	64	7	2.0	6	124	13	4.1	12
Sugar, red maple	5	1	0.3	1	10	1	0.7	2
Other hardwoods	0	0	0	0	0	0	0	0
Hemlock	0	0	0	0	0	0	0	0
All species	850	100	31.7	100	925	100	34.9	100
Parameter	$\bar{x}$		s_x	n	$\bar{x}$		s_x	n
Balsam fir								
DBH (cm)	17.6		0.50	62	20.6		1.31	17
Tree height (m) ₂	13.5		0.42	62	16.2		0.92	17
Crown position ²	2.9		0.13	62	2.5		0.27	17
Live crown length (m)	8.1		0.36	62	7.6		0.78	17
Dead crown length (m)	0.5		0.06	62	1.0		0.15	17
Proportion ₃ trees dead	0.04		0.02	62	0.14		0.08	17
site index ³	64.0			27	59.0			18
White spruce								
DBH (cm)	20.5		2.25	4	19.3		1.0	27
Tree height (m) ₂	10.7		1.45	4	15.2		0.64	27
Crown position ²	3.0		0.60	4	2.5		0.23	27
Live crown length (m)	6.0		3.70	4	6.2		0.44	27
Dead crown ₃ length (m)	0.0		0.0	4	0.6		0.06	27
site index ³	52.0			11	50.0			33

¹Includes balsam poplar

²Crown position ranking: 1-dominant, 2-co-dominant, 3-intermediate
4-suppressed

³Based on USDA Forest Service Lake States Exp. Sta. Tech. Notes 465 and 474
by S. R. Gevorkiantz

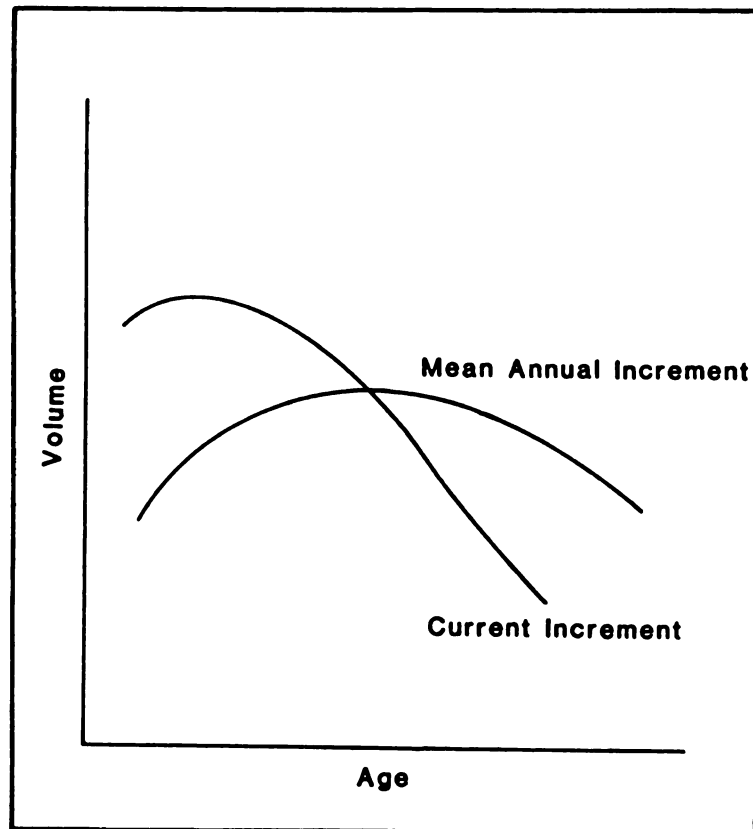


Figure 20. Relationship between the mean annual increment and the current increment in timber volume growth. The maximum mean annual increment occurs when this variable equals the current increment. This can also be shown with a first order condition since volume = $F(\text{age})$ and the mean annual increment = $F(\text{age})/\text{age}$ so $d(F(\text{age})/\text{age})/dt = (\text{age}F'(\text{age}) - F(\text{age}))/\text{age}^2 = 0 \implies F'(\text{age}) = F(\text{age})/\text{age}$ which is equivalent to the current increment equal to the mean annual increment.

stand. When determining a time to harvest, most foresters opt for maximizing the mean annual growth increment (fig. 20) (Clawson 1977). However, growth rates change slowly over a span of years. Any harvest timing which seeks to take advantage of a growth relationship can be varied without significant consequences. Further, this policy ignores forest management costs, markets for fiber, and prices for stumpage. If the objective of forest management is to maximize the volume of wood produced by a parcel of land, then this is a proper strategy. Most often, economic considerations should also be included in a harvesting decision.

The financial maturity of a stand involves costs and returns of growing timber. Three separate costs can be identified: (1) inputs of capital, labor and materials throughout the rotation of a stand; (2) interest on the returns that might be realized from the immediate harvest of a stand; and (3) rent on the bare land. Given these costs and knowledge of tree growth and future returns from this growth, the age of financial maturity can be computed. This is the point in time when net returns are maximized. The age of financial maturity will almost always be sooner than when the maximum mean annual growth increment is reached.

In practice, things are not as simple. A number of factors confound computation of financial maturity. First, the markets for the wood and the effect of the harvest volume on the market price have not been considered. Changes in either of these factors may dramatically influence the point in time when financial maturity is reached. In an extreme case, markets could cease to exist and render the concept of financial maturity meaningless. Second, the timing and intensity of harvest will partially determine the stand type and

number of trees available for the next harvest. This consideration must also be part of the harvest decision. Third, age/growth relationships are not precise. Thus, financial maturity is not a point, but an interval in time. Finally, a harvest decision may be motivated by factors other than an optimal economic return. For instance, a steady flow of fiber, minimizing loss of trees to damaging organisms, or conversion of a site to different tree species are other considerations which may dictate harvest of a forest stand.

In addition to the general considerations discussed, harvest decisions are strongly dependent upon timber ownership. There are three broad categories of timber owners: (1) small, private landowners; (2) timber firms which grow trees and use this fiber and fiber from other sources to produce a product (a vertically integrated forest firm); and (3) state or federal agencies.

Small, private forest owners are well advised to use financial maturity in deciding when to harvest. In addition, though, the owner must accept the market as given and adjust operations to it. If prices for fiber fluctuate, a strictly economic analysis of an optimal date for a timber sale is useless. Faced with the prospects of such variability, a small forest owner may seek to minimize risk by cutting prior to financial maturity.

For a vertically integrated forest firm, the cost of wood taken from the forest is a small, though not insignificant, part of total costs for processing and marketing the finished wood products. Clawson (1977) has estimated that these costs are on the order of 15% to 20% of total expenditures. As a result of operating costs, it is important that the firm continue operating at or near full capacity. This is especially true of pulp and paper plants.

Under these circumstances, low wood costs are desirable but not as important as a constant supply of wood. The vertically integrated forest firm usually chooses harvest dates within very wide limits for processing and marketing efficiency. The date of financial maturity is an important consideration, but it is not dominant in decisions about the date of harvest. These firms will cut more or less of their own timber or buy more or less from other sources for market and processing reasons and not for efficiency of growth in the forest stand.

When the Forest Service or other public agencies offer wood for sale, the market for fiber can be influenced because of the large land holdings of these agencies. In addition, the Forest Service, and perhaps other public agencies, have traditionally paid great attention to local economic stability. Judgements of timber harvest to meet these conditions may override economic and biological analysis. Finally, the Forest Service is directed through the National Forest Management Act of 1976 to grow and market timber within specific guidelines. All of these factors influence the decision as to when and how much timber to harvest.

In summary, a number of factors, other than the characteristics of stand growth and financial maturity, influence decisions to harvest timber. These considerations vary depending upon forest ownership.

For each category of timber owner, the feasibility of a partial cut strategy is strongly influenced by forest management objectives. For the small, private landowner, the principle management objective will likely be to secure the maximum economic return with the least risk. For this objective, a partial cut strategy is likely not feasible because the residual stand will probably not

increase in value faster than returns are accrued from the immediate full harvest of the stand. This is more fully explained in appendix 5. Hence, the best policy for a small, private landowner is, if possible, to completely presalvage a stand. If maximization of economic returns with least risk is not a management objective then a policy analysis for the small, private landowner is similar to that for the vertically integrated forest firm or the public agency.

For a vertically integrated forest firm or a public agency, we will assume that it is: (1) desirable to spread the harvest, marketing or processing of spruce-fir fiber over a longer time interval than would result from complete presalvage; or (2) harvest the stand to promote regeneration of multi-aged spruce-fir which is less vulnerable to budworm. Feasibility is then a question of whether a partial cut can be profitably implemented.

To determine profitability, questionnaires (appendix 6) were sent to the loggers responsible for harvesting each stand. Only one questionnaire was returned. The information from this questionnaire is given in table 9. It can be seen that the strip cut operation in stand 3 was profitable. In all likelihood, the operations in stands 1 and 2 were also profitable, since it was quite easy to secure a contractor for these harvests. Hence, a forest owner could implement a partial cut in a profitable manner. For the same reasons that a small, private landowner would likely not maximize returns from a partial harvest, neither will a vertically integrated firm or a public agency. However, as explained earlier, these forest owners do not make harvest decisions based solely on maximizing economic returns (ie; harvest at financial maturity). Forest management objectives and fiber processing and marketing considerations are also heavily

Table 9. Costs and revenues incurred by logger in harvesting stand 3.

COSTSLabor

Wages for harvesting 412 cords (\$.20/stick x 45 sticks/cord = \$9.00/cord)	3,708.00	
Employee insurance	<u>300.00</u>	
Labor cost subtotal	4,008.00	4,008.00

Equipment

Original cost ^{1/} :		
1-4500 Ford iron mule	38,700.00	
3 Husqvarna chain saws	<u>900.00</u>	
Operating costs:	39,600.00	
Capital equipment cost ^{2/}		661.15
Fuel		295.40
Maintenance		91.50
Insurance		<u>471.00</u>
Equipment cost subtotal	1,519.05	1,519.05

Transportation

Road-building costs	- 0 -	
Trucking wood to mills (hired out at \$9.00/cord)	3,708.00	
Transportation of crew to and from job site (80 mi./day)	<u>218.40</u>	
Transportation cost subtotal	3,926.40	3,926.40

Stumpage^{3/}1,392.08 1,392.08

TOTAL COSTS

10,845.53

REVENUESDelivered stumpage

Product:	Mill:	Volume in cords:	Value/cd:		
Pulpwood	Head Paper Co.	276	33.58	9,268.00	
Sawtimber	Escanaba Lumber Co.	32	35.00	1,120.00	
Products-Cedar	Habitant Fence Co.	104	35.00	<u>3,640.00</u>	
TOTAL REVENUE			14,028.00	14,028.00	
NET REVENUE					3,180.67

^{1/}Iron mule and chain saws purchased 1979.^{2/}Determination of capital cost of equipment:

$$\text{annual cost} = (\text{purchase price} - \text{salvage value}) \frac{i(1+i)^n}{(1+i)^n - 1} \quad \text{where: } i = \text{interest rate (12\%)} \\ n = \text{life of equipment in yrs.} \\ \quad \quad \quad (10 \text{ yrs. for iron mule,} \\ \quad \quad \quad 5 \text{ yrs. for chain saws)} \\ \text{salvage value} = 10\% \text{ purchase price}$$

$$\text{cost for job} = (\text{annual cost} / \text{working days per yr.}) (\# \text{ days worked on job}) \quad \text{where: } \# \text{ days worked on job} = 28 \\ (236 \text{ working days per year assumed})$$

^{3/} Species	Product	Quantity (cunits)	Price (\$/cunit)	Species Total (\$)
Balsam fir	pulpwood	35	8.90	311.50
White spruce	pulpwood	19	16.14	306.66
Cedar	products	80	5.03	402.40
Paper birch	pulpwood	58	3.94	228.52
Aspen	pulpwood	120	1.15	138.00
Mixed hardwoods	pulpwood	5	1.00	<u>5.00</u>
Sale total		317 cunits		\$1,392.08

weighed. Whether or not these objectives can be reached with this policy depend upon the dynamics of the budworm and the forest in the residual stands.

Biological Response of the System

The objective here was to assess the biological response of the system to a partial cut. To do this, budworm survival and balsam fir defoliation was evaluated in cut and control areas of each stand. Budworm survival was selected as an indicator of all the processes operating on the budworm population.

In late summer 1980, egg mass densities were estimated in the cut and control areas of stands 1 and 3. Egg mass densities were not estimated in stand 2 because the harvest of this stand had not been completed. Three branches were clipped with a pole pruner from the mid to uppercrown of 16 host trees in the cut and control areas of each stand. The number of white spruce or balsam fir sampled was based on percentage composition. From each branch, the current year's viable egg masses and parasitized egg masses were removed and recorded. If an egg mass was incompletely parasitized, those with less than half of the eggs attacked were classified as viable. Each branch was checked a second time by a different worker for overlooked egg masses. The foliage surface area of each branch was measured with a grid. Egg mass densities were converted to egg densities by assuming there were 20 eggs per viable egg mass.

In spring and summer 1981 the densities of small and large larvae, pupae, and adults were estimated in the cut and control areas in each stand. The dates for each sample and the budworm life stages sampled are given in table 10. Four branches were clipped with a pole pruner from either 5 or 10 randomly selected balsam fir trees. The foliage area was estimated similarly to the egg mass

Table 10. Dates and degree days (base 5.56 C) for five sampling periods during which spruce budworm densities were determined in three stands. Peak 3rd instar occurs at c. 167 DD, peak 6th instar at c. 416 DD and initial emergence of male moths at c. 472 DD.¹

Stand		1		2		3	
Sample		Cut	Control	Cut	Control	Cut	Control
3rd Instar	Date	6-09	6-08	6-04	6-03	6-05	6-06
	Degree Days	218	208	168	160	183	192
	Base 5.56 C						
4th Instar	Date	6-12	6-12	6-17	6-17	6-11	6-11
	Degree Days	250	250	309	309	239	239
	Base 5.56 C						
5th Instar	Date	6-23	6-23	6-19	6-19	6-18	6-18
	Degree Days	364	364	329	329	321	321
	Base 5.56 C						
Pupae S ₁	Date	7-03	7-03	7-02	7-02	7-01	7-01
	Degree Days	478	478	464	464	451	451
	Base 5.56 C						
Pupae S ₂	Date	7-08	7-08	7-07	7-08	7-07	7-07
	Degree Days	560	560	543	560	543	543
	Base 5.56 C						

¹Miller, C. A., D. C. Eidt, and G. A. McDougall. 1971. Predicting spruce budworm development. Dept. Environ. Can. For. Serv., Bi-mon. Res. Notes. 27:33-34.

sample. Samples of 3rd, 4th, and 5th instars were examined in the field and densities expressed as larvae per m^2 foliage. Larvae and pupae found during the first and second pupal samples (Pupae S_1 , Pupae S_1) were collected and reared. From these rearings, the mortality from parasitism and unknown causes was determined. Adult densities were determined from rearings and from pupal cases from which adults had emerged in the field. Defoliation of old and new foliage was estimated during the two pupal samples by classifying the percentage of foliage missing per branch into 5 groups: 0-20%, 21-40%, 41-60%, 61-80%, and 81-100%. Differences in budworm densities in the cut and uncut areas in each stand were statistically tested after necessary transformations with ANOVA. Differences in percentage mortality were tested by comparing the parameter p of a binomial distribution from the cut and control areas through a normal approximation. Defoliation estimates were tested for differences between the cut and control areas with a Mann-Whitney U test.

Dispersal loss—Estimates of budworm population densities for the different life stages sampled in the cut and control areas of stands 1, 2, and 3 are given in tables 11, 12, and 13. No significant differences in egg mass densities occurred in the cut and control areas from stands 1 and 3. Based on the close proximity and similar stand composition of the cut and control areas in stand 2, we can infer that equality of egg mass numbers likely occurred here also.

The density of feeding 3rd instars was significantly less in the control areas as compared to the cut areas in all three stands. In stands 1 and 3, this apparently indicated a greater mortality of early instars in the control areas. If egg mass densities were equivalent in the cut and control areas of stand 2, the same can be said for this plot. Since dispersal loss is apparently the major

Table 11. Density per m² balsam fir foliage of various life stages of the spruce budworm in 1981 and percentage mortality due to parasitism and unknown causes in stand 1. ANOVA (F) or a normal approximation of a binomial distribution (Z)⁰ were used to test for treatment differences. C indicates the statistic was not computed due to a small sample size.

Treatment	Control			Cut			F ₀ or Z*	P(F≥F ₀) or P(z≤Z or z≥Z)*
Sample Stage	$\bar{x}$	$S_{\bar{x}}$	n	$\bar{x}$	$S_{\bar{x}}$	n		
<u>Egg</u>								
hatched	63.01	6.20	48	62.09	5.90	48	.01	.915
parasitized	17.13	2.98	48	21.94	3.25	48	1.19	.278
<u>Larvae</u>								
3rd instar	124.31	7.80	40	218.20	14.81	40	23.56	.001
4th instar	142.37	16.64	20	191.26	25.39	20	2.60	.115
5th instar	95.72	10.13	20	111.62	16.15	20	.10	.754
4th + 5th instar	119.05	6.53	40	151.44	10.22	40	1.41	.239
<u>Pupae S₁</u>								
total	51.71	7.04	40	66.52	6.27	40	2.47	.120
larvae	14.75	2.77	40	14.96	2.43	40	.003	.955
% parasitized	.536	.059	71	.512	.054	86	0.207*	.417*
% unknown mortality	.338	.056	71	.233	.046	86	1.24 *	.108*
pupae	36.96	5.17	40	51.56	5.21	40	3.96	.050
% parasitized	.167	.025	216	.225	.025	284	1.45 *	.075*
% unknown mortality	.106	.021	216	.056	.001	284	2.00 *	.023*
adults	31.68	4.40	40	40.68	4.68	40	1.96	.166
<u>Pupae S₂</u>								
total	45.37	5.09	20	54.35	6.58	20	1.17	.287
larvae	1.84	.87	20	7.52	2.05	20	5.36	.026
% parasitized	1.0	0.0	4	.450	.111	20	C	C
% unknown mortality	0.0	0.0	4	.500	.112	20	C	C
pupae	43.53	5.44	20	46.82	5.65	20	.176	.677
% parasitized	.112	.033	89	.185	.033	135	1.35 *	.09 *
% unknown mortality	.157	.039	89	.059	.020	135	2.28 *	.01 *
adults	32.45	4.49	20	36.23	4.80	20	.332	.5681

Table 12. Density per m² balsam fir foliage of various life stages of the spruce budworm in 1981 and percentage mortality due to parasitism and unknown causes in stand 2. ANOVA (F)₀ or a normal approximation of a binomial distribution (Z)₀ were used to test for treatment differences. C indicates the statistic was not computed due to a small sample size.

Sample Stage	Control			Cut			F ₀ or Z*	P(F ₀ or Z*) or P(z ≤ Z ₀ or z ≥ Z ₀)*
	$\bar{x}$	$S_{\bar{x}}$	n	$\bar{x}$	$S_{\bar{x}}$	n		
<u>Egg</u>								
hatched								
parasitized								
<u>Larvae</u>								
3rd instar	174.19	18.48	40	276.32	22.09	40	12.57	.001
4th instar	132.09	13.09	20	201.86	19.12	20	9.96	.003
5th instar	135.05	18.37	20	137.52	11.79	20	3.60	.552
4th + 5th instar	133.57	7.04	40	169.69	7.73	40	5.74	.019
<u>Pupae S₁</u>								
total	74.50	7.31	40	66.31	6.07	40	.74	.392
larvae	12.34	1.58	40	10.98	1.96	40	.22	.592
% parasitized	.449	.060	69	.576	.061	66	1.460*	.072*
% unknown mortality	.174	.046	69	.197	.049	66	.288*	.384*
pupae	62.17	7.18	40	55.33	5.15	40	.60	.442
% parasitized	.137	.020	299	.146	.020	308	.290*	.386*
% unknown mortality	.197	.023	299	.208	.023	308	.289*	.385*
adults	44.81	4.67	40	37.04	3.86	40	1.64	.204
<u>Pupae S₂</u>								
total	85.28	12.14	20	62.12	6.27	20	1.49	.230
larvae	1.83	.89	20	1.34	.77	20	.18	.675
% parasitized	.50	.25	4	.50	.25	4	C	C
% unknown mortality	.50	.25	4	.50	.25	4	C	C
pupae	83.44	6.43	20	60.78	6.43	20	1.28	.266
% parasitized	.201	.028	209	.164	.029	165	1.489*	.068*
% unknown mortality	.072	.018	209	.079	.021	165	.241*	.405*

Table 13. Density per m² balsam fir foliage of various life stages of the spruce budworm in 1981 and percentage mortality due to parasitism and unknown causes in stand 3. ANOVA (F_0) or a normal approximation of a binomial distribution (Z) were used to test for treatment differences. C indicates the statistic was not computed due to a small sample size.

Treatment	Control			Cut			F_0 or Z*	P($F \geq F_0$) or P($z \leq Z$ or $z \geq Z$)*
Sample Stage	$\bar{x}$	$S_{\bar{x}}$	n	$\bar{x}$	$S_{\bar{x}}$	n		
<u>Egg</u>								
hatched	43.80	4.43	48	36.80	3.96	48	1.39	.241
parasitized	12.22	2.36	48	11.84	1.67	48	.228	.635
<u>Larvae</u>								
3rd instar	95.86	7.82	40	198.83	15.83	40	38.90	.001
4th instar	96.67	7.98	20	127.85	15.56	20	1.67	.204
5th instar	77.53	9.88	20	142.43	18.48	20	10.59	.002
4th + 5th instar	87.11	6.46	40	135.14	11.98	40	10.88	.002
<u>Pupae S₁</u>								
total	40.89	4.76	40	79.87	6.83	40	20.59	.001
larvae	14.24	1.95	40	32.81	3.92	40	9.07	.004
% parasitized	.467	.052	92	.635	.035	189	2.69 *	.004*
% unknown mortality	.152	.037	92	.212	.030	189	1.204*	.115*
pupae	26.65	5.88	40	47.06	5.38	40	10.55	.002
% parasitized	.114	.025	158	.142	.022	253	.829*	.203*
% unknown mortality	.165	.030	158	.198	.025	253	.850*	.198*
adults	23.80	2.93	40	35.23	3.78	40	4.98	.028
<u>Pupae S₂</u>								
total	22.96	4.57	20	37.76	6.15	20	3.34	.075
larvae	.50	.34	20	8.18	1.93	20	15.35	.001
% parasitized	1.0	0	2	.905	.064	21	C	C
% unknown mortality	0.0	0	2	.095	.064	21	C	C
pupae	22.46	4.57	20	29.57	5.89	20	.76	.390
% parasitized	.162	.036	105	.158	.042	76	.073*	.472*
% unknown mortality	.086	.027	105	.092	.033	76	.093*	.464*
adults	16.98	3.42	20	21.19	4.52	20	.165	.687

mortality factor during this period of the budworm's life cycle, the results suggest that dispersal loss was greater in the control areas. This contradicts the theoretical basis we developed for the partial cut strategy. As indicated in that section, dispersal loss of budworm has been found to increase with increases in the number of non-host trees and increases in stand openings. It is possible that stand factors which influence dispersal loss function on a finer spatial pattern than that provided by the strip and patch cuts. However, a comparison of stand parameters in the cut and control areas of each stand (tables 6, 7, and 8) provides no indications of contrasts between these areas which might explain the large differences in dispersal loss. The sampling methodology has also been reviewed in an effort to uncover a systematic bias which may have led to an underestimation of egg mass numbers in the cut areas or an overestimation in the control areas. We have found none.

The empirical evidence, therefore, seems to refute the theory which suggests that partial cuts will lower the intrinsic rate of increase of the budworm. In fact, it appears as though this rate is higher in the cut areas. However, it must be remembered that only a snapshot of a long-term process has been taken. If differences in dispersal loss are a random phenomena there is a 1-in-8 chance that observed differences occurred by chance alone. Taking into account the data presented here and that discussed previously, little is actually known of budworm dispersal. Before abandoning the idea that partial cuts can increase dispersal loss, it would be wise to collect long-term data on actual dispersal losses.

Predation and parasitism—The survival of budworm from the 3rd instar to the adult stage was less in all three cut areas than in the check areas. In fact, in

stand 2, the combined density of large larvae and pupae (Pupae S_1) is less in the cut area than in the control plot. Survival curves constructed from data in tables 11, 12, and 13 are presented in figures 21, 22, and 23. In these figures, the survival rate between successive sampling points is represented by the slope of the line joining the density estimates at these points. Survival curves in the cut areas in each stand are similar and those for the control areas in each stand are also similar. This suggests that the higher mortality rate in the cut areas may be attributable to increases in natural enemies following harvest. However, no systematic and statistically significant difference in parasitism of large larvae or pupae was found in the cut and control areas. On the other hand, it has been demonstrated that bird densities increase following a partial harvest (Titterington et al. 1979). A breeding bird census (appendix 7) in the three stands substantiates this.

Another explanation is that budworm survival is a function of density. In the cut areas, the density of 3rd instars is much greater than in the control plots. The survival of budworm between the 3rd and 4th instars is much less in the cut areas than in the controls. This suggests that survival during this period is a function of density. If true, then, at least at moderate densities, mortality during the 3rd and 4th instars compensates for mortality during the dispersal period.

Defoliation—Defoliation of old and new balsam fir foliage in the cut and control areas of each stand is given in table 14. Defoliation of the new foliage was significantly less in the cut areas of stand 2 and 3, and no difference was found in stand 1. Defoliation of old foliage was significantly less in stands 1 and 2, while no difference was found in stand 3. This data seems contradictory to the

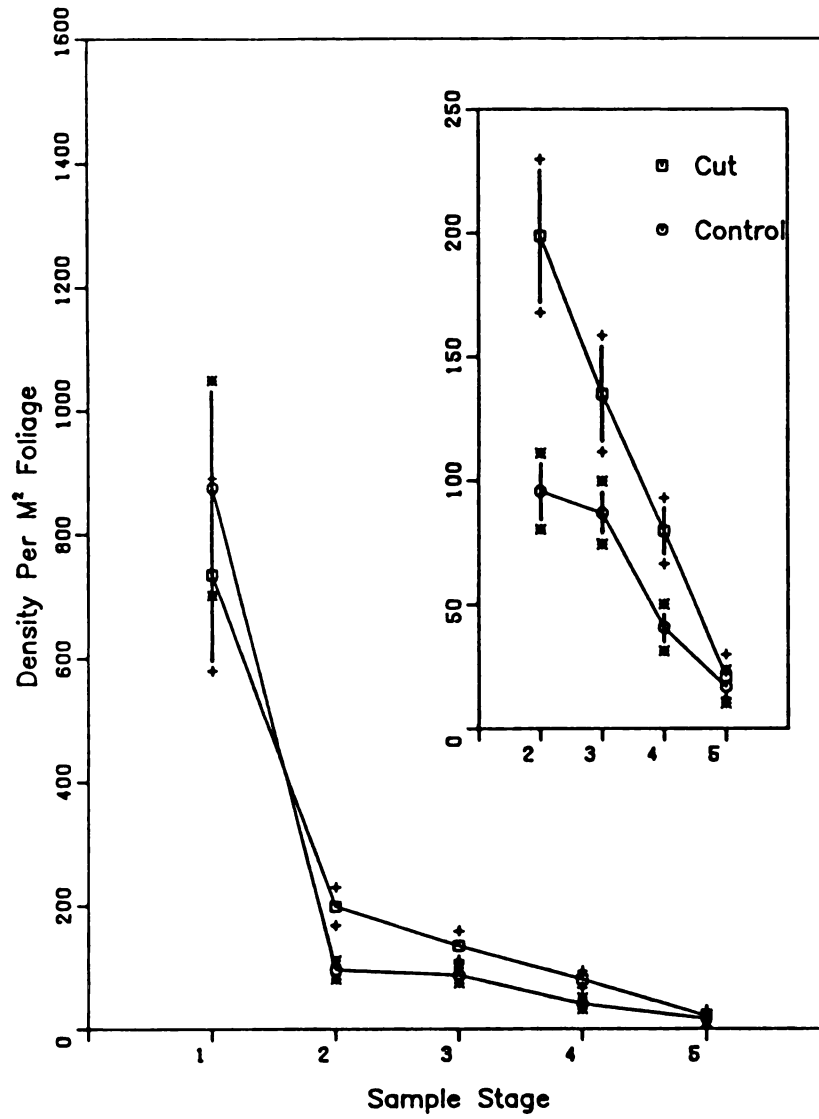


Figure 21. The density per m^2 foliage of various life stages of the spruce budworm in the cut and control areas of stand 3. The life stages are; 1-egg, 2-3rd instar, 3-4th and 5th instar, 4-6th instar and pupa, and 5-adult.

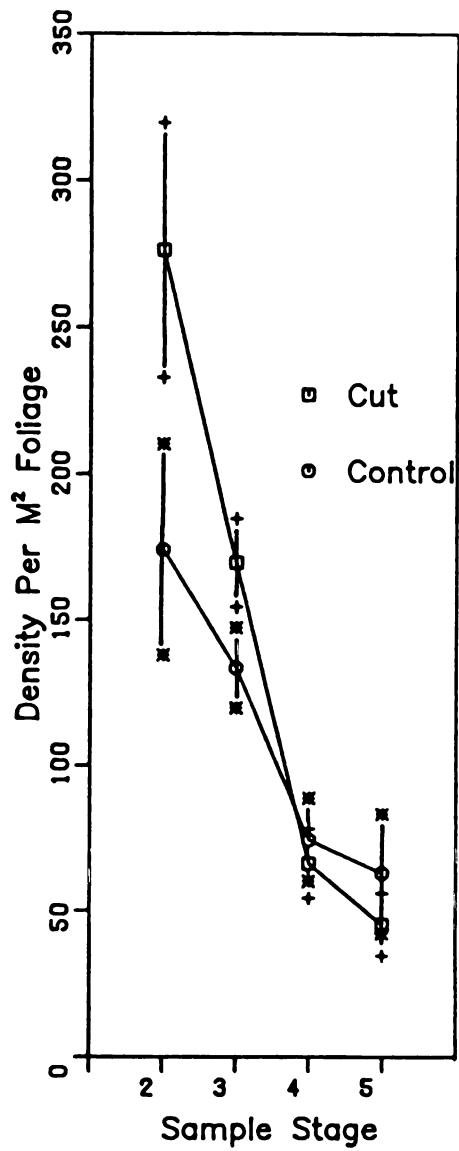


Figure 22. The density per m^2 foliage of various life stages of the spruce budworm in the cut and control areas of stand 2. The life stages are; 2-3rd instar, 3-4th and 5th instar, 4-6th instar and pupae, and 5-adult.

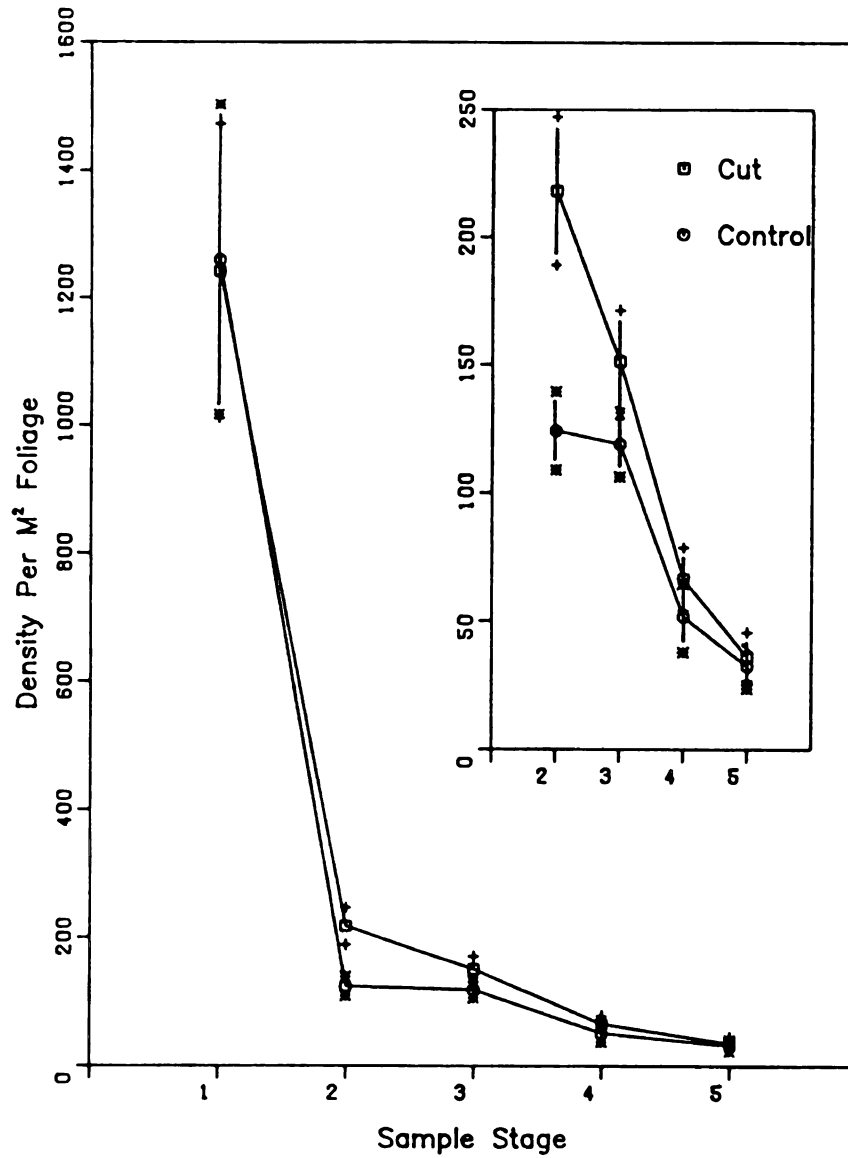


Figure 23. The density per m² foliage of various life stages of the spruce budworm in the cut and control areas of stand 1. The life stages are; 1-egg, 2-3rd instar, 3-4th and 5th instar, 4-6th instar and pupae, and 5-adult.

Table 14. Defoliation of balsam fir by spruce budworm in three stands in which part of the stand was partially harvested and the other part served as a control. Defoliation was ranked on the following scale; 0 : 0-20% foliage missing, 1 : 21-40% foliage missing, 2 : 41-60% foliage missing, 3 : 61-80% foliage missing, 4 : 81-100% foliage missing. Treatment effects were tested with the Mann-Whitney U test. The sample size in each case is 60.

Stand	Treatment	Defoliation of new foliage. ¹		Defoliation of old foliage. ²	
		$\bar{x}$	Probability of a Type I error	$\bar{x}$	Probability of a Type I error
1	cut	1.23		1.45	
	control	1.42	.6753	1.98	.0018
2	cut	1.38		1.12	
	control	1.95	.0074	1.82	.0001
3	cut	1.57		1.37	
	control	2.70	.0001	1.53	.5277

¹Defoliation occurred in 1981

²Defoliation occurred in or prior to 1981

population estimates in tables 11, 12, and 13 since most defoliation by budworm result from feeding by 5th and 6th instars. This discrepancy may result from two things. First, there may have been a systematic bias in the estimation of defoliation. Second, the cut may have influenced the trees in the residual stand in some manner to produce the observed result.

In summary, no substantiating proof of the hypothesized system response can be offered. The effect of partial cuts on the dispersal loss of budworm seems to be completely opposite from what we hypothesized. In the three stands in which a partial harvest was tested, the survival of budworm from the 3rd instar to the adult life stage was less in the cut areas. It is, however, unclear as to what caused this reduction in survival. Defoliation of old and new balsam fir foliage was generally less in the cut areas than in the control plots; however, the cause of this difference is unknown.

Conclusion

The partial harvest of spruce/fir stands has been proposed as a strategy to help reduce the impact of spruce budworm. A theoretical basis for this strategy has been developed, the feasibility of the strategy has been assessed, and a superficial check on the response of the system to the strategy has been made. At this point, sufficient information is not available to prescribe the strategy. However, when the study was initiated, there was no pretense of accomplishing such an objective.

For many years, information has been collected on the dynamics of the forest and budworm and, more recently, conceptual models have been advanced to explain these dynamics. We felt it was important to take these empirical

observations and theory and begin to mold them into a holistic strategy for dealing with the budworm problem. This report has demonstrated one way this might be done. It also serves as a basis for future work.

The major shortcoming of the proposed strategy is the unanswered question of what affect a partial harvest has on budworm and forest dynamics in the residual stands. In order for the strategy to be successful, the vulnerability of the residual stand to the budworm must be reduced. The data we collected to address this question offers no clear-cut answer. In order to adequately answer this question it will be necessary to collect information over a number of years. This is because the response of the system to a partial harvest will not be immediate and a long term series of data is indispensable for analyzing complex biological systems. Although we tried to implement the partial harvests in stands with low budworm numbers, budworm populations were well beyond the endemic level once the harvests were completed. In future work, it will be important to ensure that the strategy is implemented at low budworm densities.

Even with these shortcomings, we feel a strategy has been identified which might help forest managers deal with the spruce budworm. It certainly merits further investigation. Furthermore, the philosophy presented, that of manipulating the structure of a cropping system, should have broad applicability to other pest management problems.

Conclusions:

The results of two studies which were motivated by the concept of designing crop production systems in order to reduce the impact of crop-damaging pests have been presented. The first study explored the dynamics of an adult parasitoid and used these findings to catalyze extensions to parasitoid host theory. Three important results were generated: (1) A methodology for assessing the dynamics of adult parasitoids was developed; (2) It was demonstrated that parasitoids respond to factors in addition to the host when searching for these organisms; and (3) the attributes of a successful biological control agent were revised, the most important attribute being host searching. The theoretical results provide a foundation for further work directed toward parasitoid management. The sampling method provides a tool for acquiring information necessary for managing these biocontrol agents. In addition, this methodology might also prove useful in on-line pest management (Tummala and Haynes 1977) if it evolves to explicitly include biological control agents.

On-line pest management seeks to use models driven by monitored environmental variables to improve knowledge of the state of crop-pest systems. Biological control agents are important components of these states. Berryman (1982) has synthesized the concept of intolerant biological control agents. An intolerant biological control agent is one which is made ineffective as a result of changes in the biotic or abiotic environment. Intolerant biological control agents may give rise to thresholds which separate endemic and epidemic pest populations. Factors which contribute to intolerance are often part of the monitored environment or part of the system structure. The sampling method presented here may be used to develop models of natural enemies driven by monitored variables and can be incorporated in on-line pest management systems.

Use of the sampling method in other systems may require further development of the model used to describe parasitoid activity. In particular, daily activity patterns should be included. This is discussed with reference to another data set in appendix 7.

The second study sought to change system structure through the use of forest harvesting in order to reduce spruce budworm damage. The feasibility of this system design rested on increasing the mortality of spruce budworm in residual forest stands. Previous studies suggested that this was a likely outcome; this study, however, did not substantiate these findings.

Both studies point to a considerable gap in empirical data and theory. This gap must be bridged if design-mediated pest management is to be successful. Undoubtedly, theory cannot do for pest management what it has done for physics, chemistry, and the engineering sciences. It can, however, serve as a template upon which empirical studies can be shaped. Studies which seek to develop crop system designs will require a long-term time commitment. This is perhaps the most serious shortcoming of the spruce budworm/forest harvesting study. Currently, there is considerable difficulty in securing funding for such long-term work. Finally, many design studies will necessarily have to be conducted on endemic populations. Before this can be done, sampling and analysis methods for such studies will have to be developed.

APPENDICES

Appendix 1.

In this appendix we briefly show that if the transition of an insect from one stage to another occurs via a random time delay with no mortality within and between stages, then an aggregate approximation of a population of these transitions can be made using the probability density function of the delay. Further details can be found in Pugh (1963) and Manetsch and Park (1977).

Let $K_i^j(t)$ be an indicator variable which is equal to one if insect i enters stage j at time t and is zero otherwise. Define $u(t)$ as a unit step function such that:

$$u(t) = \begin{cases} 1 & \text{for } t > 0 \\ 0 & \text{for } t \leq 0 \end{cases}$$

Also, let τ_i be the delay in physiological time between stages j and $j + 1$ for insect i . We note that this variable is a random variable with probability density function $f(\tau)$.

For a population of n insects:

$$\begin{aligned} K_1^j(t) &= K_1^{j-1}(t-\tau_1)u(t-\tau_1) \\ K_n^j(t) &= K_n^{j-1}(t-\tau_n)u(t-\tau_n) \end{aligned} \tag{1}$$

Taking the Laplace transform of both sides of (1) produces:

$$K_i^j(s) = K_i^{j-1}(s)e^{-\tau_i s} \tag{2}$$

By summing both sides of (2) over i , assuming K_i^{j-1} and τ_i are independent and taking expectations we have:

$$E[N^j(s)] = E[N^{j-1}(u)] E[e^{-\tau s}] \quad (3)$$

where
$$N^j(s) = \sum_{i=1}^n K_i^j(s)$$

Because τ is a random variable $E[e^{-\tau s}]$ can be expressed as:

$$E[e^{-\tau s}] = \int_0^{\infty} f(\tau) e^{-\tau s} d\tau = F(s)$$

where $F(s)$ is the one-sided Laplace transform.

Substituting this result in (3) yields:

$$E[N^j(s)] = E[N^{j-1}(s)] F(s) \quad (4)$$

Multiplication in the s domain is equivalent to convolution in the time domain.

Hence, assuming $F(s)$ is time invariant (4) becomes:

$$E[n^j(t)] = \int_0^t E[n^{j-1}(z)] f(t-z) dz.$$

In other words, the expected aggregate rate of insects entering stage j is a convolution of the rate they enter stage $j-1$ and the probability density function of the time interval between these stages.

If mortality does occur within or between stages this can be easily incorporated (see Manetsch and Park 1977).

Appendix 2

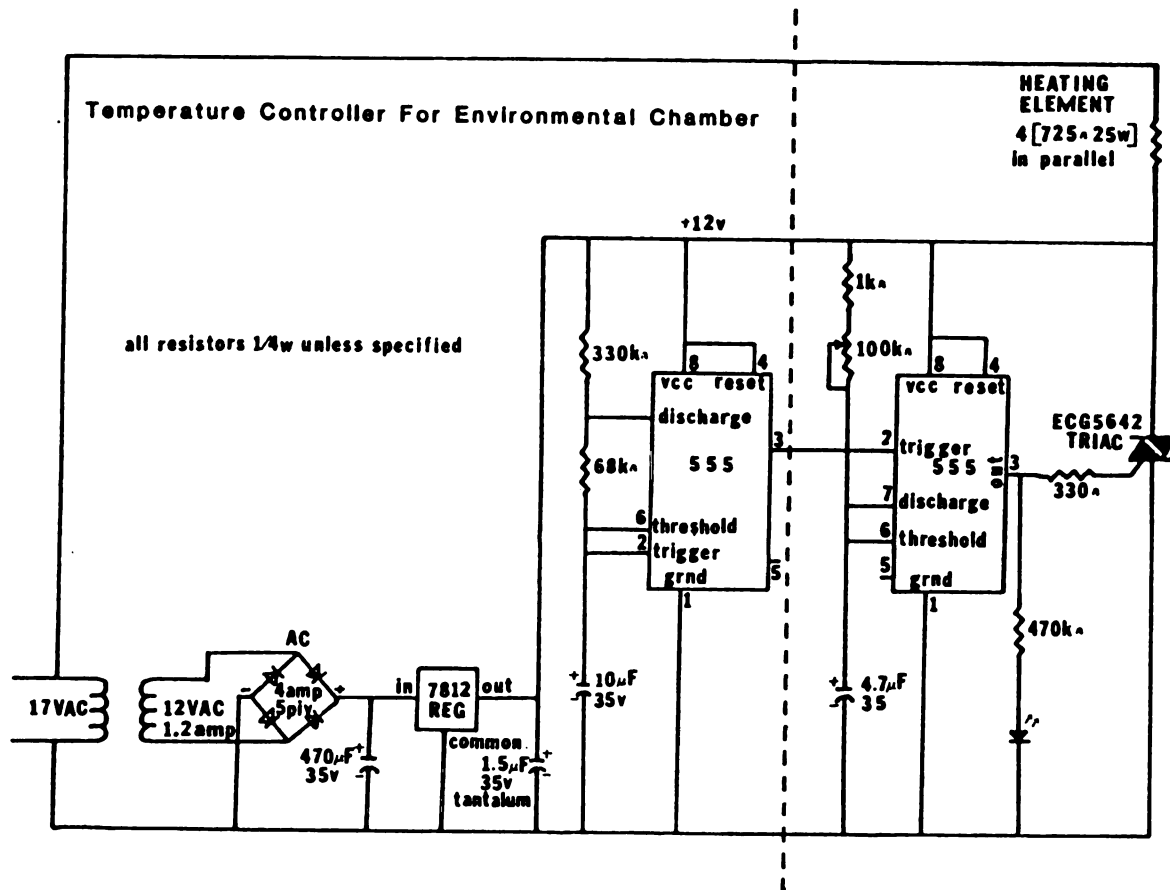


Figure 24. Circuit diagram for temperature controller of an environmental chamber. The portion to the right of the dashed line is replicated for each group of heating elements. The controller was designed by James Pieronek, Michigan State University.

Appendix 3.

In this appendix the method employed in the analysis of the parasitoid-host model is outlined. A coupled, discrete generation parasitoid-host model was given in the main text as:

$$(1) \quad \begin{aligned} H_{t+1} &= F(H_t)H_t f(P_t, H_t) \\ P_{t+1} &= H_t(1-f(P_t, H_t)) \end{aligned}$$

At equilibrium $(\bar{H}, \bar{P})$ the following conditions hold:

$$\begin{aligned} f(\bar{P}, \bar{H}) &= F^{-1} \\ \bar{P} &= \bar{H}(1-F^{-1}) \end{aligned}$$

The local stability of (1) can be determined by examining the dynamics of a perturbation model defined as

$$(2) \quad \begin{aligned} x_{t+1} &= F(\bar{H} + x_t)(\bar{H} + x_t)f(\bar{P} + y_t, \bar{H} + x_t) - F(\bar{H})\bar{H}f(\bar{P}, \bar{H}) \\ y_{t+1} &= (\bar{H} + x_t)(1 - f(\bar{P} + y_t, \bar{H} + x_t)) - \bar{H}(1 - f(\bar{P}, \bar{H})) \end{aligned}$$

and linearized about $\bar{H}$ and $\bar{P}$.

For stability, $x(t)$ and $y(t) \longrightarrow 0$ as $t \longrightarrow \infty$.

The linearized model obtained through a Taylor expansion and after substitution of equilibrium conditions is given as

$$\begin{bmatrix} x_{t+1} \\ y_{t+1} \end{bmatrix} = \begin{bmatrix} 1 + F(\bar{H})\bar{H}F(\bar{H})^{-1} + F(\bar{H})\bar{H}\frac{\partial f}{\partial H^*} & \bar{H}F(\bar{H})\frac{\partial f}{\partial P^*} \\ 1 - F(\bar{H})^{-1} - \bar{H}\frac{\partial f}{\partial H^*} & -\bar{H}\frac{\partial f}{\partial P^*} \end{bmatrix} \begin{bmatrix} x_t \\ y_t \end{bmatrix}$$

||

(A)

A necessary and sufficient condition for stability of the linearized model is that the dominant eigenvalue of matrix A has modulus less than 1.

For model (5) in the text an equilibrium value for $\bar{H}^*$ can be found by solving the function

$$H\Psi\left(1 + \frac{aH(\Psi-1)}{\Psi K}\right)^{-k} - H = 0$$

where $\Psi = \lambda \exp[-\gamma H/(\alpha^2 + H^2)]$. This was done using Newton's method for determining the roots of an equation. An equilibrium value for $\bar{P}^*$ can then be easily found using the equilibrium conditions. Matrix A for model (5) is given as

$$A = \begin{bmatrix} 1 - \frac{(\alpha^2 - H^2)\gamma H}{(\alpha^2 + H^2)^2} & H\left(1 + \frac{aP}{k}\right)^{-1} a \\ 1 - \left(1 + \frac{aP}{k}\right)^{-k} & H\left(1 + \frac{aP}{k}\right)^{-(k+1)} a \end{bmatrix} \bigg|_{\substack{* \\ H \\ P}}$$

The stability region can be found by solving (2) through simulation for various values of x_t and y_t .

Appendix 4.

Computer program listings.

```

*JOB CARD*,JC2000, RG2. 100
ATTACH,B,BNPGCOMPLEX. 110
FTN. 120
LOAD,B. 130
LGO. 140
*EOS 150
C THIS PROGRAM USES AN OPTIMAZATION ALGORITHM TO ASSIGN VALUES 160
C TO PARAMETERS OF A MODEL DESCRIBED IN SUBROUTINE FUNC. THE 170
C OPTIMIZATION ALGORITHM IS BOX'S COMPLEX ALGORITHM DESCRIBED IN; 180
C 190
C          KEUSTER, J.L., AND J.H. MIZE. 1973. OPTIMIZATION 200
C          TECHNIQUES WITH FORTRAN. MCGRAW-HILL, NEW YORK. 500PP. 210
C 220
C REQUIRED DATA IS CONTAINED IN THE SUBROUTINES AND AT THE END OF 230
C THE PROGRAM AS FOLLOWS 240
C 250
C CARD  COLUMNS  CONTENTS 260
C 1      1 - 5      N (NUMBER OF VARIABLES) 270
C 1      6 - 10     M (NUMBER OF CONSTRAINTS) 280
C 1     11 - 15     K (NUMBER OF POINTS IN COMPLEX) 290
C 1     16 - 20     ITMAX (MAXIMUM ITERATIONS) 300
C 1     21 - 25     IC (NUMBER OF IMPLICIT VARIABLES) 310
C 1     26 - 30     IPRINT (PRINT CONTROL) 320
C 2      1 - 10     ALPHA (REFLECTION FACTOR) 330
C 2     11 - 20     BETA (CONVERGENCE PARAMETER) 340
C 2     21 - 25     GAMMA (CONVERGENCE PARAMETER) 350
C 3      1 - 8      INITIAL X(1) 360
C 3      9 - 16     INITIAL X(2) 370
C 3     17 - 24     INITIAL X(3) 380
C 3     25 - 32     INITIAL X(4) 390
C 4      1 - 8      G(1) (LOWER CONSTRAINT) 400
C 4      .          . 410
C 5      1 - 8      H(1) (UPPER CONSTRAINT) 420
C 5      .          . 430
C SUBROUTINE FUNC 440
C 450
C PURPOSE 460
C MODEL OF MALAISE TRAP CATCH OF GLYPHTA FUMIFERANAE WHICH 470
C IS BASED ON THE TEMPORAL CHANGES IN THE NUMBER OF ADULTS 480
C AND WEATHER FACTORS WHICH INFLUENCE ADULT ACTIVITY. THE 490
C SUBROUTINE IS USED BY THE OPTIMIZATION ALGORITHM TO FIT 500
C PARAMETERS TO THE MODEL; 510
C CATCH=(PROPOR*AW)*FLYAD 520
C WHERE; 530
C PROPOR IS A PROPORTIONALAIITY CONSTANT 540
C A IS A VECTOR OF PARAMETERS TO BE DETERMINED 550
C W IS A VECTOR OF WEATHER FACTORS 560
C FLYAD IS THE DENSITY OF ADULT G. FUMIFERANAE 570
C THE INITIAL INPUT (PUPIN) IS ARBITRARY AS THE VARIABLES IN THE 580
C MODEL ARE SCALED ACCORDING TO THIS VALUE 590
C 600
C DESCRIPTION OF SUBROUTINE PARAMETERS 610
C N - NUMBER OF EXPLICIT INDEPENDENT VARIABLES 620
C M - NUMBER OF CONSTRAINTS 630
C K - NUMBER OF POINTS IN COMPLEX 640
C X - INDEPENDENT VARIABLES (PARAMETERS TO BE FITTED TO MODEL) 650
C F - OBJECTIVE FUNCTION 660
C I - POINT INDEX 670
C 680
C DESCRIPTION OF VARIABLES USED IN SUBROUTINE 690
C RP, RA1 - INTERMEDIATED RATES IN DISTRIBUTED DELAYS 700
C NDD48 - DEGREE DAYS BASE 48F PER DAY 710
C PRECIP - PRECIPTATION IN INCHES BETWEEN 800 AND 2200 HRS 720

```

```

C CALL DELAYS WHICH MODEL THE PUPAL AND ADULT LIFE STAGE
CALL DELAY2(ADULT,RMORT,RA1,DELAD,DT,KAD)
CALL DELAY2(PUPIN,ADULT,RP,DELPUP,DT,KPUP)
C COMPUTE STORAGE IN DELAYS WHICH IS THE NUMBER OF PUPAE OR
C ADULTS AT ANY POINT IN TIME (PUP,FLYAD)
VAR1=VAR2=0.
DO 15 J=1,KPUP
15  VAR1=VAR1+RP(J)
DO 16 J=1,KAD
16  VAR2=VAR2+RA1(J)
PUP=DELPUP/KPUP*VAR1
FLYAD=DELAD/KAD*VAR2
IF (I2.EQ.NN1) FLYAD2=FLYAD
PUPIN=0.
20  CONTINUE
C COMPUTE MULTIPLIER TO RELATE TRAP CATCH, ADULT DENSITY AND
C EXTRINSIC FACTORS
RMULT=PROPOR+(ALPHA*PRECIP(I1))+(BETA*TEMP(I1))
IF (RMULT.LT.0) RMULT=0.
CATCH=RMULT*FLYAD2
C COMPUTE OBJECTIVE FUNCTION
U=U+(CATCH-TRUCAT(I1))*2
F(I)=-U
10  CONTINUE
END

C
C
C
SUBROUTINE DELAY2 (RINR,ROUTR,CROUTR,DEL,DT,K)
DIMENSION CROUTR(1)
DEL1=DEL/(FLOAT(K)*DT)
RIN=RINR
DO 1 I=1,K
ABC=CROUTR(I)
CROUTR(I)=ABC+(RIN-ABC)/DEL1
1  RIN=ABC
ROUTR=CROUTR(K)
RETURN
END

C
C
C
C SUBROUTINE CONST
C
C PURPOSE
C SPECIFIES EXPLICIT AND IMPLICIT CONSTRAINT LIMITS. IT
C MUST BE INCLUDED EVEN IF NO IMPLICIT CONSTRAINTS ARE USED.
C PARAMETERS ARE DEFINED ABOVE.
C
SUBROUTINE CONST(N,M,K,X,G,H,I)
DIMENSION X(20,20),G(20),H(20)
RETURN
END

*EOS
4      4      8      100      0      0
      1.3      50.0      5
180.0    0.75    0.0    0.0
110.0    0.0     -2.0    0.0
250.0    2.0     2.0     2.0
*EOP

```

```

PROGRAM BOX(INPUT,OUTPUT)
DIMENSION X(20,20),R(20,20),F(20),G(20),H(20),XC(20)
INTEGER GAMMA
KOUNT=0
1 READ 1,N,M,K,ITMAX,IC,IPRINT
2 FORMAT (8I5)
3 READ 2, ALPHA,BETA,GAMMA
4 FORMAT(2E10.4,I5)
5 DELTA=0.0001
6 READ 4, (X(1,J),J=1,N)
7 READ 4, (G(I),I=1,M)
8 READ 4, (H(I),I=1,M)
9 FORMAT(9F8.4)
10 DO 100 II=2,K
11 DO 3 JJ=1,N
12 R(II,JJ)=RANF(1.0)
13 CONTINUE
14 PRINT 10
15 FORMAT(1H1,/,18X,24HCOMPLEX PROCEDURE OF BOX)
16 PRINT 18
17 FORMAT(/,2X,10HPARAMETERS )
18 PRINT 11,N,M,K,ITMAX,IC,ALPHA,BETA,GAMMA,DELTA
19 O11 FORMAT (/,2X,4HN = ,I2,3X,4HM = ,I2,3X,4HK = ,I2,2X,8HI23
20 +TMAX = ,
21 1I4,2X,5HIC = ,I2,/,2X,8HALPHA = ,F5.2,5X,7HBETA = ,F10.24
22 +5.3X,
23 28HGAMMA = ,I2,3X,8HDELTA = ,F6.5)
24 PRINT 900
25 FORMAT(/,2X,16HINITIAL X VALUES)
26 DO 200 J = 1,N
27 PRINT 16, J, X(1,J)
28 CONTINUE
29 50 CALL CONSX (N,M,K,ITMAX,ALPHA,BETA,GAMMA,DELTA,X,R,F,IT,
30 1IEV2,NO,G,H,XC,IPRINT)
31 IF (IT-ITMAX) 20,20,30
32 20 PRINT 14, F(IEV2)
33 O14 FORMAT (///,2X,30HFINAL VALUE OF THE FUNCTION = ,E20.8)
34 PRINT 15
35 O15 FORMAT (/,2X,14HFINAL X VALUES)
36 DO 300 J=1,N
37 PRINT 16, J, X(IEV2,J)
38 O16 FORMAT (/,2X,2HX(.I2,4H) = ,E20.8)
39 300 CONTINUE
40 PRINT 9, IT
41 9 FORMAT (//* THE NUMBER OF ITERATIONS IS *, I5)
42 GO TO 999
43 30 PRINT 17, ITMAX
44 O17 FORMAT (///,2X,38HTHE NUMBER OF ITERATIONS HAS EXCEEDED
45 +,I4,10X,
46 118HPROGRAM TERMINATED)
47 999 STOP
48 END
49 SUBROUTINE CONSX (N,M,K,ITMAX,ALPHA,BETA,GAMMA,DELTA,X,R,
50 +,F,
51 1IT,IEV2,NO,G,H,XC,IPRINT)
52 DIMENSION X(20,20),R(20,20),F(20),G(20),H(20),XC(20)
53 INTEGER GAMMA
54 IT = 1
55 KODE = 0
56 IF (M-N) 20,20,10
57 10 KODE = 1
58 20 CONTINUE
59 DO 40 II=2,K

```

```

DO 30 J=1,N
30 X(II,J) = 0.0
40 CONTINUE
DO 65 II=2,K
DO 50 J=1,N
I = II
CALL CONST (N,M,K,X,G,H,I)
X(II,J) = G(J) + R(II,J)*(H(J)-G(J))
50 CONTINUE
K1 = II
CALL CHECK (N,M,K,X,G,H,I,KODE,XC,DELTA,K1)
IF (II-2) 51, 51, 55
51 IF (IPRINT) 52,65,52
52 PRINT 18
018 FORMAT (//,2X,30HCOORDINATES OF INITIAL COMPLEX)
IO = 1
PRINT 19, (IO, J, X(IO,J), J=1,N)
019 FORMAT (/,3(2X,2HX(,I2,1H, ,I2,4H) = ,1PE13.6))
55 IF (IPRINT) 56,65,56
56 PRINT 19, (II, J, X(II,J), J=1,N)
65 CONTINUE
K1 = K
DO 70 I=1,K
CALL FUNC(N,M,K,X,F,I)
70 CONTINUE
KOUNT=1
IA=0
IF(IPRINT) 72,80,72
72 PRINT 21
21 FORMAT(/,2X,22HVALUES OF THE FUNCTION )
PRINT 22, (J,F(J), J=1,K)
22 FORMAT(/,3(2X,2HF(,I2,4H) = ,1PE13.6))
80 IEV1=1
DO 100 ICM=2,K
IF(F(IEV1)-F(ICM)) 100,100,90
90 IEV1=ICM
100 CONTINUE
IEV2=1
DO 120 ICM=2,K
IF(F(IEV2)-F(ICM)) 110,110,120
110 IEV2=ICM
120 CONTINUE
IF(F(IEV2)-(F(IEV1)+BETA)) 140,130,130
130 KOUNT=1
GO TO 150
140 KOUNT=KOUNT+1
IF(KOUNT-GAMMA) 150,240,240
150 CALL CENTR(N,M,K,IEV1,I,XC,X,K1)
DO 160 JJ=1,N
160 X(IEV1,JJ)=(1.0+ALPHA)*(XC(JJ))-ALPHA*(X(IEV1,JJ))
I=IEV1
CALL CHECK(N,M,K,X,G,H,I,KODE,XC,DELTA,K1)
CALL FUNC(N,M,K,X,F,I)
170 IEV2=1
DO 190 ICM=2,K
IF(F(IEV2)-F(ICM)) 190,190,180
180 IEV2=ICM
190 CONTINUE
IF(IEV2-IEV1) 220,200,220
200 DO 210 JJ=1,N
X(IEV1,JJ)=(X(IEV1,JJ)+XC(JJ))/2.0

```

210	CONTINUE	121
	I=IEV1	122
	CALL CHECK(N,M,K,X,G,H,I,KODE,XC,DELTA,K1)	123
	CALL FUNC(N,M,K,X,F,I)	124
	GO TO 170	125
220	CONTINUE	126
	IF (IPRINT) 230,228,230	127
230	PRINT 23,IT	128
23	FORMAT(//.2X,17HITERATION NUMBER ,I5)	129
	PRINT 24	130
24	FORMAT(/.2X,30HCOORDINATES OF CORRECTED POINT)	131
	PRINT 19, (IEV1,JC,X(IEV1,JC), JC=1,N)	132
	PRINT 21	133
	PRINT 22, (I,F(I),I=1,K)	134
	PRINT 25	135
25	FORMAT(/.2X,27HCOORDINATES OF THE CENTROID)	136
	PRINT 26, (JC,XC(JC),JC=1,N)	137
26	FORMAT(/.3(2X,2HX(.I2,6H.C) = .1PE14.6,4X))	138
228	IT=IT+1	139
	IF (IT-ITMAX) 80,80,240	140
240	RETURN	141
	END	142
	SUBROUTINE CHECK(N,M,K,X,G,H,I,KODE,XC,DELTA,K1)	143
	DIMENSION X(20,20),G(20),H(20), XC(20)	144
10	KT=0	145
	CALL CONST(N,M,K,X,G,H,I)	146
	DO 50 J=1,N	147
	IF(X(I,J)-G(J)) 20,20,30	148
20	X(I,J)= G(J)+DELTA	149
	GO TO 50	150
30	IF(H(J)-X(I,J)) 40,40,50	151
40	X(I,J)=H(J)-DELTA	152
50	CONTINUE	153
	IF(KODE)110,110,60	154
60	NN=N+1	155
	DO 100 J=NN,M	156
	CALL CONST(N,M,K,X,G,H,I)	157
	IF(X(I,J)-G(J)) 80,70,70	158
70	IF(H(J)-X(I,J))80,100,100	159
80	IEV1=I	160
	KT=1	161
	CALL CENTR (N,M,K,IEV1,I,XC,X,K1)	162
	DO 90 JJ=1,N	163
	X(I,JJ) = (X(I,JJ) +XC (JJ))/2.0	164
90	CONTINUE	165
100	CONTINUE	166
	IF (KT) 110, 110, 10	167
110	RETURN	168
	END	169
	SUBROUTINE CENTR (N,M,K,IEV1,I,XC,X,K1)	170
	DIMENSION X(20,20),XC(20)	171
	DO 20 J=1,N	172
	XC(J) = 0.0	173
	DO 10 IL=1,K1	174
10	XC(J) = XC(J) + X(IL,J)	175
	RK=K1	176
20	XC(J) = (XC(J)-X(IEV1,J))/(RK-1.0)	177
	RETURN	178
	END	179

```

      PROGRAM STABLE (INPUT,OUTPUT)
C THIS PROGRAM COMPUTES THE REGION OF STABILITY FOR STABLE
C EQUILIBRIA OF THE FOLLOWING MODEL:
C    $H(T+1)=H(T) \exp(-BH(T)/C+2+H(T)+2)(1+AP/K)+-K$ 
C    $P(T+1)=H(T)(1-(1+AP/K)+-K)$ 
C DATA REQUIREMENTS ARE EQUILIBRIA VALUES AND VALUES FOR
C PARAMETERS AND ARE INPUT IN DATA STATEMENTS.
C THE STABILITY REGION IS DETERMINED ITERATIVELY BY
C PERTURBING HE BY SOME VALUE DELTA AND CHECKING THROUGH
C SIMULATION CONVERGENCE OF THE MODEL BACK TO HE AND PE.
C PRECISION IS DETERMINED BY THE TEST VALUE OF DO LOOP 1.
C K=0 FLAGS K=INFINITY
      DIMENSION DRK(4),DA(4),DHE(4,4),DPE(4,4)
      DATA DRK/.75,2.0,6.0,0.0/
      DATA DA/1.5,2.0,2.5,3.0/
      DATA (DHE(1,M),M=1,4)/1.12039,.85213,.73440,.66097/,
+ (DHE(2,M),M=1,4)/.91802,.73042,.62695,.55780/,
+ (DHE(3,M),M=1,4)/.85923,.68300,.58156,.51270/
+ , (DHE(4,M),M=1,4)/.83137,.65886,.55793,.48903/
      DATA (DPE(1,M),M=1,4)/.39855,.30951,.29494,.28999/,
+ (DPE(2,M),M=1,4)/.32348,.29462,.28796,.28280/,
+ (DPE(3,M),M=1,4)/.31079,.29133,.28484,.27710/
+ , (DPE(4,M),M=1,4)/.30607,.28987,.28281,.27422/
      Y=10.0
      B=3.75
      C=1.0
      DO 300 L=1,4
      DO 301 M=1,4
      RK=DRK(L)
      A=DA(M)
      HS=DHE(L,M)
      PS=DPE(L,M)
      PRINT 100, B,C,Y,A,RK,HS,PS
100  FORMAT ("OB=",F4.2,1X,"C=",F3.1,1X,"Y=",F4.1,1X,"A=",F3.
+1,1X,
+ "RK=",F3.1,1X,"HE=",F7.5,1X,"PE=",F7.5)
      PRINT 101
101  FORMAT ("OMAX HOST AND PARASITE DENSITIES FOR WHICH MODE
+L IS STABL
+E")
      SIGMA=.05
      DO 1 I=1,20
      DO 2 I2=1,2
      SIGN=1.
      IF(I2.EQ.2)SIGN=-1.
      P1=PS+(SIGMA*I*SIGN)
      IF(P1.LT.O.) GO TO 21
      P=P1
      CHECK=5*HS
      DO 3 J=1,2
      SIGN=1.
      IF(J.EQ.2)SIGN=-1.
      DELTA=.05
      H1=HS
4    CONTINUE
      DELTA=DELTA*2
      H3=HS+(DELTA*SIGN)
      IF(H3.LT.O.) H3=.001
      H=H3
      CALL DYNAM (P,H,INDEX,Y,B,C,RK,A,CHECK)
      P=P1
      IF(INDEX.EQ.1) GO TO 4
5    CONTINUE

```

```

        IF(H3.LT.H1) VAR1=H1-H3          710
        IF(H1.LT.H3) VAR1=H3-H1          720
        IF(VAR1.LT..005) GO TO 6          730
        H2=(H1+H3)/2                     740
        H=H2                             750
        CALL DYNAM (P,H,INDEX,Y,B,C,RK,A,CHECK) 760
        P=P1                             770
        IF(INDEX.EQ.1) H1=H2             780
        IF(INDEX.EQ.0) H3=H2             790
        GO TO 5                           800
6      CONTINUE                          810
        PRINT 102,P1,H1                  820
102    FORMAT (" PARASITE DENSITY= ",F7.5,"HOST DENSITY= ",F7.5830
+ )                                       835
3      CONTINUE                          840
        GO TO 25                         850
21     CONTINUE                          860
        PRINT 22                         870
22     FORMAT (" PARASITE DENSITY LESS THAN ZERO") 880
25     CONTINUE                          890
2      CONTINUE                          900
1      CONTINUE                          910
301    CONTINUE                         920
300    CONTINUE                         930
        END                             940
C                                           950
C                                           960
C                                           970
        SUBROUTINE DYNAM (P,H,INDEX,Y,B,C,RK,A,CHECK) 980
        INDEX=1                          990
        DO 1 I=1,100                    1000
        IF(RK.EQ.0.) GO TO 10           1010
        V=(1/(1+A*P/RK))*RK            1020
        GO TO 11                       1030
10     CONTINUE                         1040
        V=EXP(-A*P)                     1050
11     CONTINUE                         1060
        P=H*(1-V)                       1070
        H=H*Y*EXP(-B*H/((C**2)+(H**2)))*V 1080
        IF(H.GT.CHECK) INDEX=0         1090
1      CONTINUE                         1100
        RETURN                          1110
        END                             1120

```

```

PROGRAM EIGENV (INPUT,OUTPUT)
C THIS PROGRAM COMPUTES THE EIGENVALUES OF THE FOLLOWING PARASITE
C HOST MODEL LINEARIZED ABOUT THE EQUILIBRIUM POINT
C  $H(T+1)=H(T)YEXP(-BH(T)/C**2+H(T)**2)((1+AP/K)**-K)$ 
C  $P(T+1)=H(T)(1-(1+AP/K)**-K)$ 
C DATA REQUIREMENTS ARE VALUES FOR ALL PARAMETERS AND EQUILIBRIUM
C DENSITY OF THE HOST POPULATION (K=0 FLAGS INFINITY, H=0 FLAG INFINITY)
C EQUILIBRIUM)
  DIMENSION DC(3),DRK(4),DA(5),DH(3,4,5)
  DATA (DH(1,1,I),I=1,5)/.66097,.7344,.85213,1.12039,0./,
  + (DH(1,2,I),I=1,5)/.5578,.62695,.73042,.91902,1.53906/,
  + (DH(1,3,I),I=1,5)/.5127,.58156,.683,.85923,1.32473/,
  + (DH(1,4,I),I=1,5)/.48903,.55793,.65886,.83137,1.25647/,
  + (DH(2,1,I),I=1,5)/.76831,.86262,1.02186,1.47683,0./,
  + (DH(2,2,I),I=1,5)/.61619,.69588,.81580,1.03479,1.74045/,
  + (DH(2,3,I),I=1,5)/.55489,.63154,.74510,.94161,1.44326/,
  + (DH(2,4,I),I=1,5)/.52304,.59908,.71039,.89939,1.34973/,
  + (DH(3,1,I),I=1,5)/.55807,.61367,.69855,.86409,0./,
  + (DH(3,2,I),I=1,5)/.49852,.55404,.64030,.79407,1.29533/,
  + (DH(3,3,I),I=1,5)/.46634,.52631,.61441,.76741,1.18364/,
  + (DH(3,4,I),I=1,5)/.45033,.51133,.60064,.75400,1.14571/
  DATA DA/3.,2.5,2.,1.5,1./
  DATA DC/1.,1.1,.9/
  DATA DRK/.75,2.,6.,0./
  Y=10.
  B=3.75
  DO 1 L=1,3
  DO 2 M=1,4
  DO 3 N=1,5
  FLAG=0.
  C=DC(L)
  RK=DRK(M)
  A=DA(N)
  H=DH(L,M,N)
  PRINT 10,C,RK,A,H
10  FORMAT ("OC= ",F3.1,1X,"K= ",F4.2,1X,"A= ",F3.1,1X,"HOST
  + EQUIL= ",F7.3)
  IF(H.EQ.0.) GO TO 100
C COMPUTE PARASITE EQUIL. DENSITY
  F=Y*EXP(-B*H/((C**2)+(H**2)))
  P=((F-1)/F)*H
C COMPUTE FOUR TERMS OF MATRIX FOR LINEARIZED MODEL
  SIGN=-1
  X=C**2
  V=H**2
  T11=(1-(((X-V)*B*H)/((X+V)**2)))*SIGN
C IF K=INFINITY USE POISSON ZERO TERM
  IF(RK.EQ.0.) GO TO 110
  W=(A*P/RK)+1
  T12=H*A/W
  T21=(1-((1/W)**RK))*SIGN
  T22=(((1/W)**(RK+1))*H*A)*SIGN
  GO TO 120
110 CONTINUE
  W=-A*P
  T12=W*H*SIGN
  T21=(1-EXP(W))*SIGN
  T22=H*EXP(W)*A*SIGN
120 CONTINUE
C TERMS OF QUADRATIC EQUATION

```

```

      QT1=((T11+T22)/2.)*SIGN          640
      QI1=T11*T22                      650
      QI2=T12*T21                      660
      QI3=QI1-QI2                      670
      QI4=((QT1*2)**2)-(4*QI3)          680
      IF(QI4.LT.O.) FLAG=1              690
      IF(QI4.LT.O.) QI4=QI4*SIGN        700
      QT2=(SQRT(QI4))/2                 710
      PRINT 20,QT1,QT2                  720
20   FORMAT("OEIGENVALUES= ",F7.5,1X,"PLUS AND MINUS",1X,F7.5730
+ )                                     735
      IF(FLAG.EQ.O.) GO TO 3            740
      PRINT 30                          750
30   FORMAT (" PLUS AND MINUS TERM IS COMPLEX") 760
      GO TO 3                           770
100  CONTINUE                          780
      PRINT 40                          790
40   FORMAT (" NO EQUIL. FOUND, NO EIGENVALUES COMPUTED") 800
3    CONTINUE                          810
2    CONTINUE                          820
1    CONTINUE                          830
      END                              840

```

Appendix 5.

In this appendix we show why a partial cutting strategy is probably not compatible with maximizing economic returns with least risk. The return (R_t) from the sale of a tract of timber at time t is determined by price (P_t) and volume (V_t):

$$R_t = P_t \cdot V_t \quad (1)$$

We will assume that the only costs associated with growing timber are foregone returns from immediate harvest of the trees. (The conclusions reached will be the same even if this is not true). The value (Val_t) of a stand at some future point in time (t) is then given by:

$$Val_t = R_t - R_{t_0} e^{i(t-t_0)} \quad (2)$$

In (2), R_{t_0} are the current returns and i is the interest rate obtained on investments. The exponential function is used to approximate the future value of the current stand.

Suppose some proportion (δ) of the stand is harvested prior to a budworm outbreak where $0 \leq \delta \leq 1$. Then (2) can be written as:

$$Val_t = (1 - \delta)R_t + (2\delta - 1)R_{t_0} e^{i(t-t_0)} \quad (3)$$

The rate at which the value of the stand increases is given by:

$$\frac{dVal_t}{dt} = (1 - \delta) dR_t/dt + (2\delta - 1)iR_{t_0} e^{i(t-t_0)} \quad (4)$$

This is a complicated function; however, its general nature can be determined by evaluating three harvesting policies.

If the complete stand is harvested at time t_0 , then $\delta = 1$, and (4) becomes:

$$dVal_t/dt = iR_{t_0} e^{i(t-t_0)} \quad (5)$$

The rate of increase of the stand is equal to the rate of return on an investment. If it is possible to harvest the stand, this policy entails no risk.

If none of the stand is harvested prior to the outbreak, (4) becomes:

$$dVal_t/dt = dR_t/dt - iR_{t_0}e^{i(t-t_0)} \quad (6)$$

In order that the rate of increase in value be positive, price and volume must increase in combination at a rate faster than returns are accrued from an immediate harvest. This is an unlikely situation since the volume of spruce fir stands greater than 50 years in age generally increases at a rate less than or equal to 5% of the present volume (Bowman 1944). This increase may decline or even be less than zero during a budworm outbreak. It is even more improbable that this policy will be superior to the first one or:

$$dR_t/dt > 2iR_{t_0}e^{i(t-t_0)} \quad (7)$$

If half of the stand is harvested prior to an outbreak, (4) becomes:

$$dVal_t/dt = .5dR_t/dt \quad (8)$$

For this policy to be superior to the first one, equation (7) must be satisfied. Once again, this is unlikely. Therefore, complete presalvage is the best strategy for maximizing returns and minimizing risks.

Appendix 6.

Form sent to loggers to determine costs and returns of harvests.

Location:

Sale number:

Logger:

Please fill in the blanks as accurately as possible. Write an (X) by those estimates you consider to be very rough estimates.

A. Wages

1. Number of people employed in the harvest of this sale area _____
2. Number of days spent working in this area _____
3. Hourly wage rate and total 'man-hours' worked at each rate

<u>wage rate</u>	<u>total hours</u>	<u>wage rate</u>	<u>total hours</u>
1) _____	_____	4) _____	_____
2) _____	_____	5) _____	_____
3) _____	_____	6) _____	_____
4. Insurance cost (Workman's Comp.) _____
5. Other wages: _____

B. Equipment

1. What equipment was used to harvest this sale area?
 - a) _____
 - b) _____
 - c) _____
 - d) _____
 - e) _____

Please itemize costs 2-6 for each equipment item above:

2. Investment in equipment (original cost)

a) _____	d) _____
b) _____	e) _____
c) _____	

3. Fuel cost

a) _____ d) _____
 b) _____ e) _____
 c) _____

4. Maintenance cost

a) _____ d) _____
 b) _____ e) _____
 c) _____

5. Insurance cost (for equipment)

a) _____ d) _____
 b) _____ e) _____
 c) _____

6. Depreciation charged to equipment per year

a) _____ d) _____
 b) _____ e) _____
 c) _____

7. Scheduled operating hours: _____

8. Approximate down-time in % _____

C. Transportation

1. Road-building cost (if any) _____

2. Other costs in this category: _____

D. Revenues

1. Name and location of mill(s) that sawlogs, pulpwood, or chips were sold to:

2. Total volume removed (mill scale)

<u>product</u>	<u>volume</u>	<u>value</u>
pulpwood	_____	_____
sawlogs	_____	_____
other,	_____	_____
_____	_____	_____

3. Other revenues: _____

Appendix 7.

Bird census data for stands 1, 2 and 3.

KEY TO BIRD CODES -----

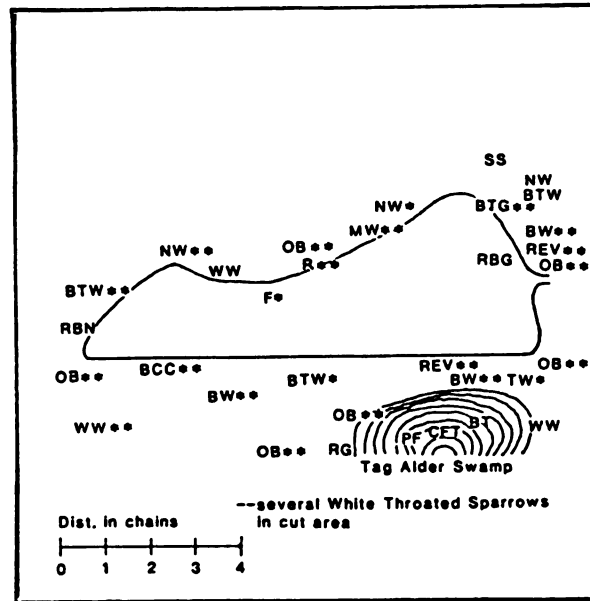
AF	- Alder Flycatcher	OB	- Ovenbird
NTW	- Black and White Warbler	PF	- Purple Finch
BB	- Blackburnian Warbler (or BW)	PS	- Pine Siskin
BC	- Brown Creeper	PW	- Palm Warbler
BCC	- Black Capped Chickadee (or CD)	PWP	- Pileated Woodpecker
BHC	- Brown Headed Cowbird	R	- Robin
BT	- Bittern	RBG	- Rose Breasted Grosbeak
BTG	- Black Throated Green Warbler	RBN	- Red Breasted Nuthatch (or NH)
BW	- Blackburnian Warbler (or BB)	REV	- Red Eyed Vireo
CMW	- Cape May Warbler	RG	- Ruffed Grouse
CS	- Chipping Sparrow	RS	- Red Start
SCW	- Chestnut sided Warbler	SS	- Song Sparrow
CYT	- Common Yellow Throat (or YT)	ST	- Scarlet Tanager
DW	- Downy Woodpecker	SV	- Solitary Vireo
EP	- Eastern Pheobe	TW	- Tennessee Warbler
EWP	- Eastern Wood Peewee	V	- Veery
F	- Flicker	WC	- Woodcock
GCK	- Golden Crowned Kinglet	WT	- Wood Thrush
HT	- Hermit Thrush	WTS	- White Throated Sparrow
HWP	- Hairy Woodpecker	WW	- Winter Wren
IB	- Indigo Bunting	YBC	- Yellow Billed Cuckoo
MGW	- Magnolia Warbler	YBSS	- Yellow Bellied Sapsucker
MW	- Mourning Warbler	YRW	- Yellow Rumped Warbler
NH	- Nuthatch (or RBN)	YT	- Common Yellow Throat (or CYT)
NW	- Nashville Warbler		

Legend for Bird Sighting Maps

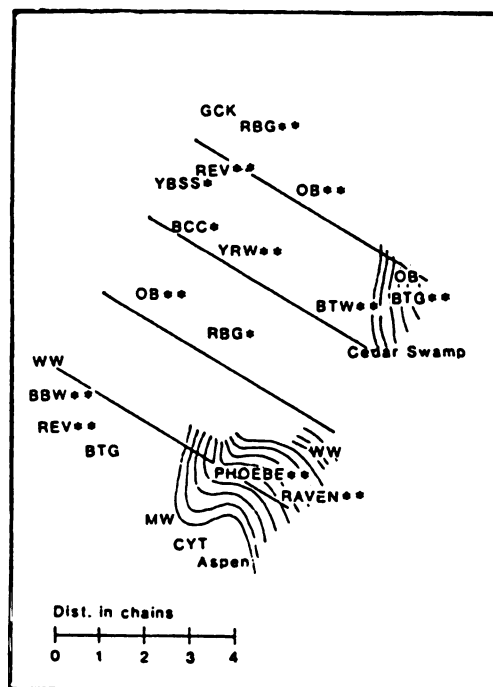
- aa - One sighting
- aa* - Two sightings
- aa** - Territory confirmed

Methods: The bird census was conducted by mapping singing males. This was done by transecting each plot on 6-1, 6-3 and 6-4, 1981.

Stand 1.

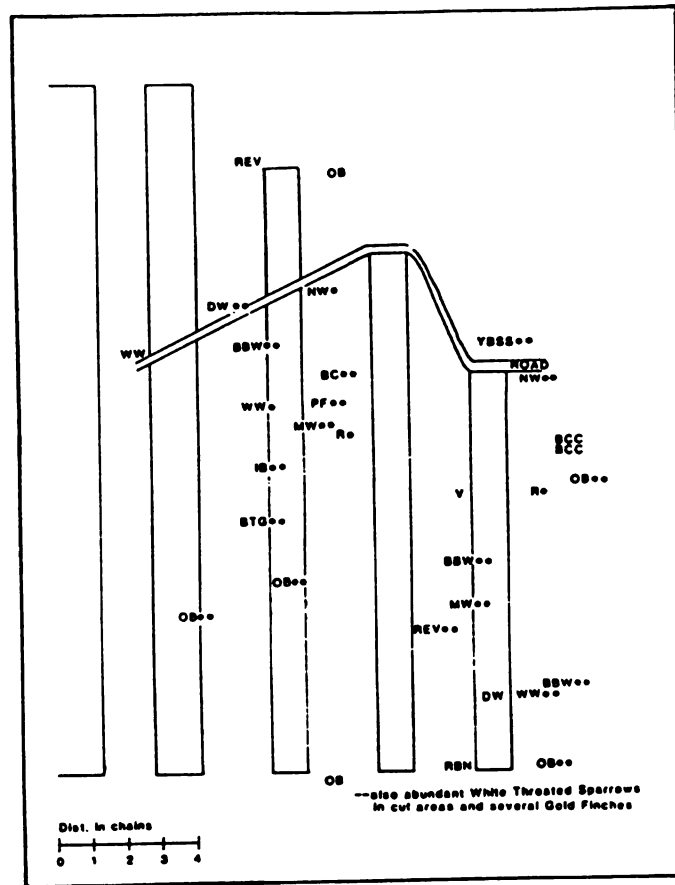


Cut

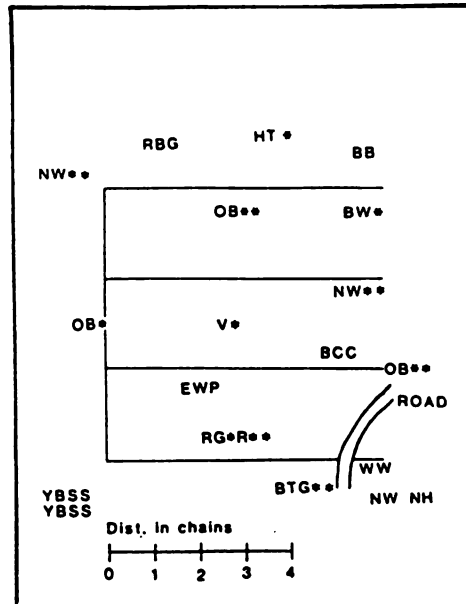


Control

Stand 2.

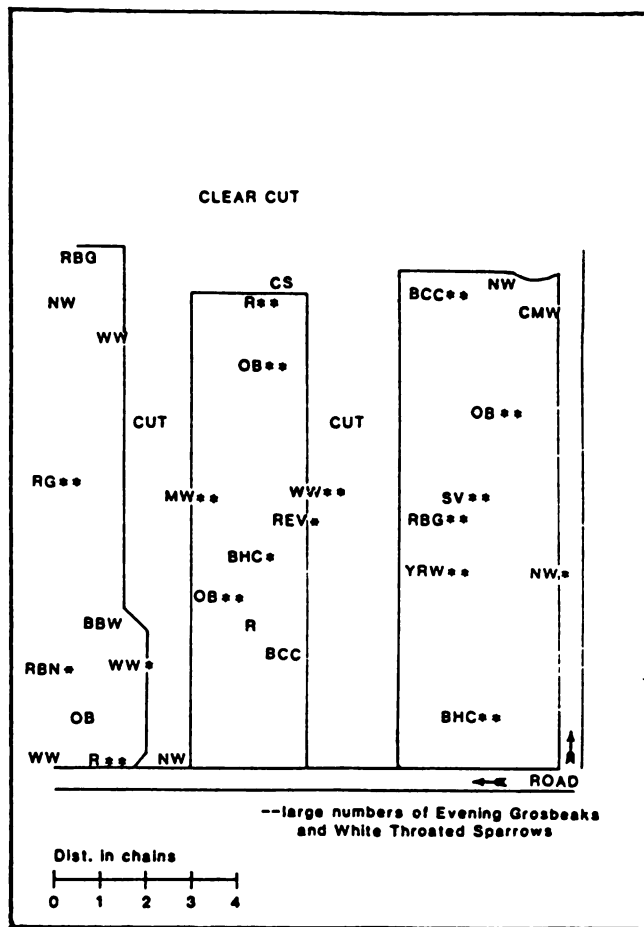


Cut

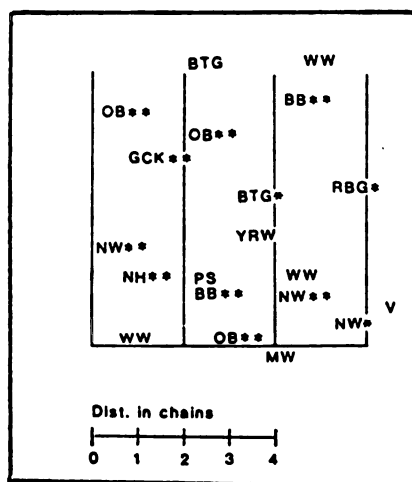


Control

Stand 3.



Cut



Control

Appendix 8.

The malaise traps and method presented for analyzing data collected by these traps can be used with other parasitoids. It may be necessary, though, to base the model on the daily activity of these animals. This was unnecessary with G. fumiferanae attacking spruce budworm because most adult activity occurred during an identifiable part of the day. As a result, average temperature and total rainfall during this time period were good measures of adult activity.

Data on G. fumiferanae attacking jack pine budworm (Elliot, unpubl.) indicate that, in this habitat, G. fumiferanae is active throughout the day (fig. 25). When this data and appropriate weather information (table 15) were inserted in the model, a poor fit was obtained. One reason model parameters could not be fit to this data was that rain often fell for only part of the day while the rest of the day was conducive to parasitoid activity (i.e., 1068 DD and 1091 DD, table 15). This did not happen in the spruce fir habitat. In order for the model to work, weather (or other influencing variables) and trap catch must be assessed at regular intervals throughout each day. The part of the model which predicts adult parasitoid density will still be appropriate, but activity must be modeled as a convolution of density, intrinsic activity patterns (if any), and factors (i.e., weather) which influence activity.

The inability of the model to describe the data collected on G. fumiferanae in jack pine does not contradict the idea that parasitoid activity patterns are strongly influenced by weather. This data was collected from two locations and is plotted as a function of degree days (base 8.9°C) in figure 26. The pattern of trap catch is similar in both plots. This similarity can be evaluated statistically.

Let $x_1(i)$ equal 1 if the trap catch on day i is greater than the catch on day $i-1$, and 0 if it is less in one of the two locations. The variable $x_2(i)$ is defined similarly for the other location. No pattern is expected between x_1 and x_2 when adult parasitoid density is relatively constant if weather does not influence trap catch. If $x_1(i)$ and $x_2(i)$ are equal then let $x_{12}(i)$ be 1, and 0 otherwise. The variable x_t , defined as the summation of $x_{12}(i)$ over i , is a binomial random variable. A test of a relationship between x_1 and x_2 is whether p of this distribution equals 0.5. Ignoring trap catch prior to c. 70% emergence of the adult female parasitoids (< 1037 DD) and the tail end of trap catch (> 1477 DD) $x_t = 17$ and the sample size (N) = 23. Using a one-sided test (we expect $p > 0.5$) the probability of this occurring is .017 ($p(x_t \geq 17); x_t \sim (B, N = 23, p = .5)$). The null hypothesis ($p = 0.5$) is rejected. Hence, the pattern of trap catch in the two locations is similar, which suggests that weather influenced G. fumiferanae's adult activity. This is reinforced by the observation that the dramatic decline in parasitoid activity at 1263 DD was accompanied by prolonged cool, wet weather.

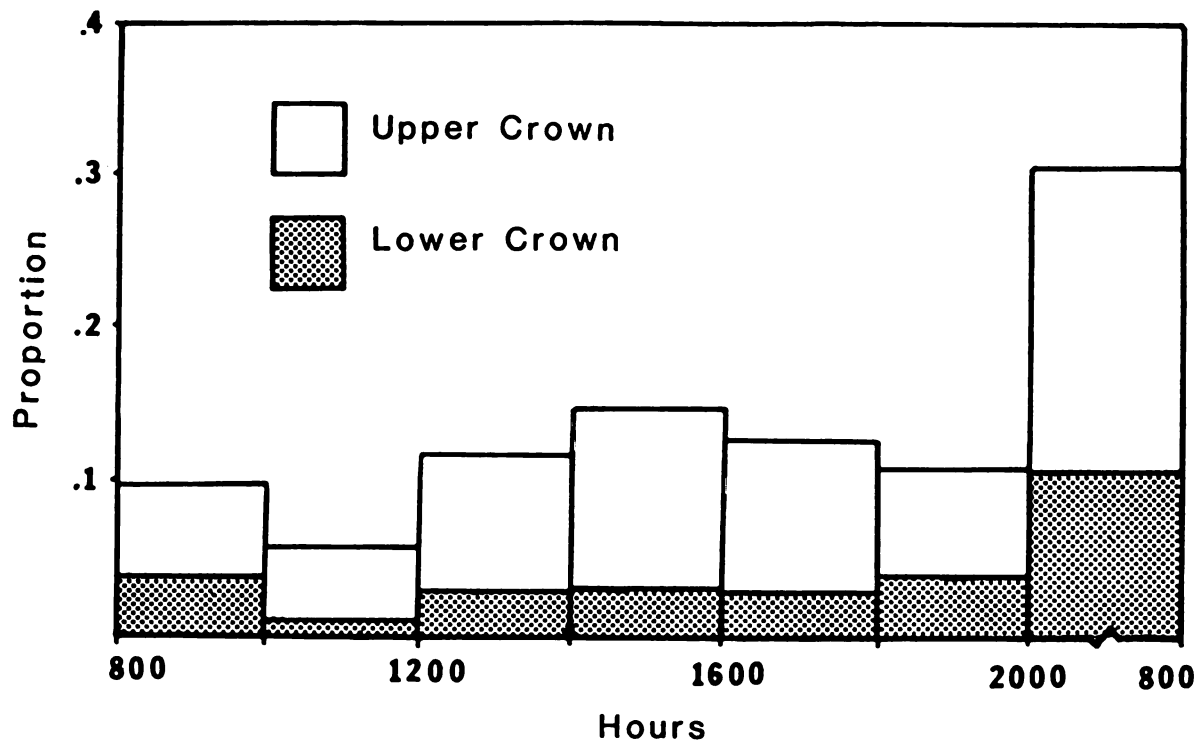


Figure 25. Proportion of total malaise trap catch of female *Glypta fumiferanae* for 7 time intervals within a day. The sample period was 6 days (7-19 to 7-24). One trap was located in 48 jack pine trees. Twenty four traps were in the upper crown and 24 in the lower crown. Data collected by N. Elliott in Grand Traverse Co., MI.

Table 15. Malaise trap catch of female Glypta fumiferanae from two plots and weather data in 1982. One trap was located in 24 jack pine in each plot. Twelve traps were in the upper crown and 12 in the lower crown. Data collected by N. Elliott in Grand Traverse Co., MI.

Julian Date	Degree Days Base 8.9° C.	Malaise Trap Catch		Temperature ¹	Precipitation ²
		1	2		
191	924	0	1	25.78	.97
192	938	0	0	16.85	.58
193	955	2	4	20.78	0
194	972	4	12	25.63	0
195	991	10	11	23.74	.03
196	1012	22	28	27.21	0
197	1037	35	15	29.67	0
198	1068	14	30	27.15	7.85
199	1091	45	28	23.71	.76
200	1106	28	19	20.44	0
201	1122	33	25	21.71	0
202	1137	54	38	24.56	0
203	1160	40	31	22.89	0
204	1181	64	30	24.37	0
205	1200	92	54	26.74	0
206	1225	41	43	26.11	.03
207	1249	35	24	22.29	.03
208	1263	4	3	18.07	1.04
209	1276	9	9	21.82	0
210	1289	25	4	23.41	0
211	1309	39	25	21.33	0
212	1329	27	17	22.71	0
213	1350	20	20	23.26	0
214	1369	14	8	20.37	0
215	1392	28	22	24.26	0
216	1416	10	14	20.74	0
217	1435	13	11	22.11	0
218	1455	11	6	23.52	0
219	1477	19	9	26.29	0
220	1498	6	2	24.48	0
221	1510	3	2	15.48	.08
222	1517	5	1	15.93	0
223	1528	0	1	17.89	0
224	1537	1	1	19.48	0
225	1551	0	0	21.67	0

¹average °C between 800 and 2200 hours

²total precipitation in cm. between 800 and 2200 hours

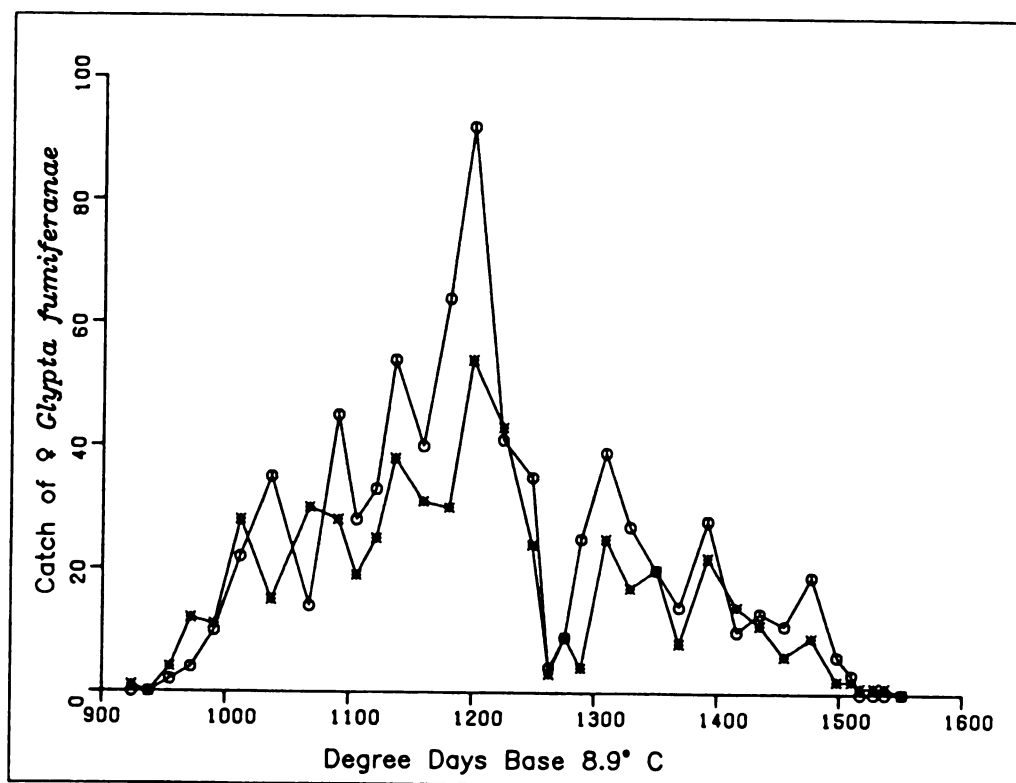


Figure 26. Malaise trap catch of female *Glypta fumiferanae* from two plots in relation to degree days base 8.9°C. in 1982. One trap was located in each of 24 jack pine in each plot. Twelve traps were in the upper crown and 12 in the lower crown. Data collected by N. Elliott in Grand Traverse Co., MI.

Appendix 9.

Spruce budworm population estimation data from forest harvesting study

9.1 Egg mass densities in stands 1 and 3.

Description by columns; 1-stand, 2-treatment; (1) cut, (2) control, 3-blank, 4 and 5-tree, 6-blank, 7-branch, 8-blank, 9-species; (1) balsam fir, (2) white spruce, 10-blank, 11 through 14-branch surface area (cm^2), 15-blank, 16 and 17-hatched egg masses, 18-blank, 19 and 20-parasitized egg masses. Repeat 3 times.

9.2 Early and mid instar densities in stands 1, 2 and 3.

Description by column: 1-stand, 2-treatment; (1) cut, (2) control, 3-sample number, 4-blank, 5 through 7-date, 8-blank, 9 and 10-tree, 11-branch, 12-blank, 13 and 14-budworm, 15 blank, 16 through 19-branch surface area (100 cm^2). Repeat 2 times.

9.3 Late instar, pupal and adult densities in stands 1, 2, 3.

Description by columns: 1-stand, 2-treatments; (1) cut, (2) control, 3-sample number, 4 and 5-tree, 6-blank, 7-branch, 8-blank, 9 and 10-branch surface area (100 cm^2), 11-blank, 12-defoliation of all foliage; (0) 0-20%, (1) 21-40%, (2) 41-60%, (3) 51-80%, (4) 81-100%, 13-defoliation of new foliate (same ranking), 14-blank, 15 and 16-adults, 17-blank, 18-parasitized pupae, 19-blank, 20-pupal mortality (unknown cause), 21-blank, 22 and 23-Meteorus trachynotus pupae, 24-blank, 25-G. fumiferanae pupae, 26-blank, 27-Apanteles fumiferanae pupae, 28 and 29-blank, 30 and 31-total budworm at time of sample, 32-blank, 33 and 34-larvae at time of sample, 35-blank, 36 and 37-parasitized larvae, 38-blank, 39-larval mortality (unknown cause). Repeat.

9.1

11 01 1 1 0900 05 01	12 06 1 2 2050 05 01	31 10 2 2 2050 05 02	32 14 3 1 0900 02 02
11 01 2 1 0600 03 00	12 06 2 2 1900 05 00	31 10 3 2 1200 04 08	32 15 1 1 0900 02 00
11 01 3 1 0750 03 02	12 06 3 2 2100 13 09	31 11 1 2 1500 04 03	32 15 2 1 0800 00 00
11 02 1 1 1500 06 01	12 07 1 1 1500 05 04	31 11 2 2 1250 03 03	32 15 3 1 0800 00 01
11 02 2 1 1300 06 02	12 07 2 1 1400 06 00	31 11 3 2 1500 06 00	32 16 1 2 1800 06 03
11 02 3 1 0650 06 00	12 07 3 1 1200 01 00	31 12 1 2 1800 07 04	32 16 2 2 1100 03 01
11 03 1 1 1000 03 00	12 08 1 1 1050 07 00	31 12 2 2 1600 05 06	32 16 3 2 1500 06 01
11 03 2 1 0900 04 01	12 08 2 1 1200 06 03	31 12 3 2 1150 08 03	
11 03 3 1 1050 09 00	12 08 3 1 1200 01 00	31 13 1 2 0850 05 00	
11 04 1 1 2200 08 01	12 09 1 1 0800 04 00	31 13 2 2 0800 04 00	
11 04 2 1 1100 01 02	12 09 2 1 0800 05 01	31 13 3 2 1200 04 00	
11 04 3 1 1700 12 02	12 09 3 1 1000 14 04	31 14 1 2 1500 02 00	
11 05 1 1 1600 05 00	12 10 1 1 0600 03 00	31 14 2 2 1700 08 00	
11 05 2 1 0500 02 00	12 10 2 1 0850 05 00	31 14 3 2 0800 05 01	
11 05 3 1 0800 05 00	12 10 3 1 0850 02 01	31 15 1 2 1750 03 01	
11 06 1 1 2400 02 03	12 11 1 1 0950 06 01	31 15 2 2 1000 00 01	
11 06 2 1 2100 04 00	12 11 2 1 0650 09 01	31 15 3 2 1900 00 00	
11 06 3 1 1200 04 00	12 11 3 1 0350 05 01	31 16 1 2 2400 10 04	
11 07 1 1 1000 04 02	12 12 1 1 1300 03 02	31 16 2 2 1100 07 00	
11 07 2 1 2100 08 02	12 12 2 1 2300 22 11	31 16 3 2 1600 14 01	
11 07 3 1 1500 00 01	12 12 3 1 1000 04 02	32 01 1 1 1400 01 00	
11 08 1 1 1200 08 05	12 13 1 1 0900 03 04	32 01 2 1 2000 05 01	
11 08 2 1 1400 05 02	12 13 2 1 0800 08 02	32 01 3 1 0950 00 00	
11 08 3 1 1700 07 02	12 13 3 1 1300 12 09	32 02 1 1 0800 01 01	
11 09 1 1 0900 10 02	12 14 1 1 1000 04 01	32 02 2 1 1200 03 02	
11 09 2 1 0500 03 05	12 14 2 1 0850 03 01	32 02 3 1 0850 08 01	
11 09 3 1 0900 07 06	12 14 3 1 0900 05 02	32 03 1 1 2100 19 03	
11 10 1 1 1200 06 01	12 15 1 1 1200 04 05	32 03 2 1 2100 15 05	
11 10 2 1 1500 09 01	12 15 2 1 0800 02 00	32 03 3 1 1400 05 02	
11 10 3 1 1400 12 03	12 15 3 1 0900 05 01	32 04 1 1 0800 08 02	
11 11 1 1 1050 14 01	12 16 1 1 1200 10 03	32 04 2 1 1100 07 03	
11 11 2 1 0800 04 01	12 16 2 1 0900 03 00	32 04 3 1 1900 06 08	
11 11 3 1 1400 06 04	12 16 3 1 0900 10 00	32 05 1 1 2300 15 05	
11 12 1 1 1050 08 01	31 01 1 2 2100 15 01	32 05 2 1 1900 10 01	
11 12 2 1 1100 05 01	31 01 2 2 1150 11 01	32 05 3 1 1900 13 03	
11 12 3 1 0750 05 06	31 01 3 2 1000 06 02	32 06 1 1 2700 11 05	
11 13 1 1 1000 23 04	31 02 1 2 2250 16 03	32 06 2 1 1600 09 06	
11 13 2 1 1000 06 00	31 02 2 2 1200 08 00	32 06 3 1 1050 04 00	
11 13 3 1 1000 04 01	31 02 3 2 2100 13 05	32 07 1 1 1400 05 01	
11 14 1 1 1800 16 03	31 03 1 1 0800 01 01	32 07 2 1 1800 12 02	
11 14 2 1 0800 03 00	31 03 2 1 1500 04 01	32 07 3 1 1000 09 04	
11 14 3 1 1500 25 02	31 03 3 1 1800 02 00	32 08 1 1 2100 13 03	
11 15 1 1 1900 17 02	31 04 1 1 1050 06 05	32 08 2 1 2150 11 00	
11 15 2 1 1600 11 03	31 04 2 1 1300 02 01	32 08 3 1 1850 07 04	
11 15 3 1 1200 13 04	31 04 3 1 1050 02 01	32 09 1 1 0900 01 03	
11 16 1 1 1500 15 02	31 05 1 1 2600 06 00	32 09 2 1 0800 01 00	
11 16 2 1 2000 32 06	31 05 2 1 2000 03 01	32 09 3 1 1900 02 03	
11 16 3 1 1500 13 06	31 05 3 1 1500 05 04	32 10 1 1 1000 04 00	
12 01 1 1 1300 01 03	31 06 1 1 1500 04 00	32 10 2 1 0600 00 00	
12 01 2 1 0800 10 06	31 06 2 1 1000 03 00	32 10 3 1 1250 02 02	
12 01 3 1 1400 07 08	31 06 3 1 2400 11 00	32 11 1 1 0700 04 01	
12 02 1 1 0900 09 00	31 07 1 1 1800 01 01	32 11 2 1 1150 08 00	
12 02 2 1 0750 14 05	31 07 2 1 1950 06 00	32 11 3 1 1100 03 00	
12 02 3 1 0650 06 02	31 07 3 1 1400 06 01	32 12 1 1 1900 02 00	
12 03 1 1 1500 05 10	31 08 1 2 1000 14 05	32 12 2 1 0850 04 00	
12 03 2 1 0800 07 06	31 08 2 2 1300 10 04	32 12 3 1 1200 04 02	
12 03 3 1 2200 22 10	31 08 3 2 1250 18 01	32 13 1 1 1800 01 02	
12 04 1 1 0600 06 01	31 09 1 2 1200 07 03	32 13 2 1 1000 04 00	
12 04 2 1 0500 02 00	31 09 2 2 1550 03 02	32 13 3 1 1200 01 01	
12 04 3 1 1200 02 03	31 09 3 2 0900 04 00	32 14 1 1 0900 01 00	
12 05 1 2 1800 04 02	31 10 1 2 1400 09 08	32 14 2 1 0800 00 00	
12 05 2 2 1200 05 00			
12 05 3 2 2000 16 02			

9.2

111 608 011 55 17.0	113 623 014 10 09.5	122 612 022 14 09.5
111 608 012 21 07.5	113 623 021 17 12.0	122 612 023 12 08.0
111 608 013 15 09.0	113 623 022 11 06.0	122 612 024 06 06.0
111 608 014 22 07.0	113 623 023 01 06.0	122 612 031 13 12.0
111 608 021 29 15.0	113 623 024 09 15.0	122 612 032 16 11.0
111 608 022 22 12.0	113 623 031 24 10.0	122 612 033 13 12.0
111 608 023 16 09.5	113 623 032 28 14.0	122 612 034 11 12.0
111 608 024 12 11.5	113 623 033 08 09.0	122 612 041 27 12.0
111 608 031 32 12.0	113 623 034 16 18.0	122 612 042 11 10.0
111 608 032 45 15.5	113 623 041 06 18.0	122 612 043 19 10.0
111 608 033 36 09.0	113 623 042 05 17.0	122 612 044 42 19.0
111 608 034 42 11.0	113 623 043 13 16.0	122 612 051 21 13.5
111 608 041 21 11.0	113 623 044 05 15.0	122 612 052 11 04.0
111 608 042 30 13.5	113 623 051 19 14.0	122 612 053 18 05.5
111 608 043 27 12.0	113 623 052 18 13.0	122 612 054 19 13.0
111 608 044 18 06.0	113 623 053 21 16.0	123 623 011 10 14.0
111 608 051 42 12.0	113 623 054 17 06.0	123 623 012 07 11.5
111 608 052 11 11.5	121 609 011 22 11.0	123 623 013 09 12.0
111 608 053 17 09.0	121 609 012 22 16.0	123 623 014 03 07.0
111 608 054 18 08.0	121 609 013 22 09.0	123 623 021 05 09.0
111 608 061 41 12.0	121 609 014 20 13.0	123 623 022 02 08.0
111 608 062 22 08.5	121 609 021 08 07.0	123 623 023 03 17.0
111 608 063 36 14.0	121 609 022 14 15.0	123 623 024 15 12.0
111 608 064 22 11.0	121 609 023 08 08.0	123 623 031 13 12.0
111 608 071 22 08.0	121 609 024 06 09.0	123 623 032 16 11.0
111 608 072 25 12.0	121 609 031 17 10.0	123 623 033 13 12.0
111 608 073 32 10.5	121 609 032 24 18.0	123 623 034 11 12.0
111 608 074 44 13.0	121 609 033 08 06.5	123 623 041 24 16.0
111 608 081 16 18.5	121 609 034 09 08.0	123 623 042 18 10.0
111 608 082 04 12.0	121 609 041 11 18.5	123 623 043 06 10.0
111 608 083 09 12.0	121 609 042 15 12.0	123 623 044 25 20.0
111 608 084 08 14.0	121 609 043 14 12.0	123 623 051 21 15.0
111 608 091 34 14.0	121 609 044 20 14.0	123 623 052 21 17.0
111 608 092 16 09.5	121 609 051 16 11.0	123 623 053 11 16.0
111 608 093 30 17.5	121 609 052 07 09.0	123 623 054 07 05.0
111 608 094 21 12.0	121 609 053 18 12.0	
111 608 101 13 10.0	121 609 054 06 07.0	
111 608 102 26 13.0	121 609 061 07 11.0	
111 608 103 20 13.0	121 609 062 03 10.0	
111 608 104 09 05.0	121 609 063 04 13.5	
112 612 011 10 07.0	121 609 064 10 14.0	
112 612 012 14 17.0	121 609 071 16 12.0	
112 612 013 13 07.5	121 609 072 10 09.0	
112 612 014 12 09.5	121 609 073 08 10.5	
112 612 021 21 14.0	121 609 074 19 09.0	
112 612 022 12 10.0	121 609 081 14 08.0	
112 612 023 15 09.0	121 609 082 16 11.0	
112 612 024 04 09.5	121 609 083 16 10.0	
112 612 031 32 19.5	121 609 084 06 10.0	
112 612 032 09 06.0	121 609 091 26 15.0	
112 612 033 15 11.0	121 609 092 09 13.0	
112 612 034 13 12.0	121 609 093 29 18.0	
112 612 041 65 16.5	121 609 094 16 08.0	
112 612 042 66 13.0	121 609 101 17 12.0	
112 612 043 30 08.0	121 609 102 14 12.5	
112 612 044 38 15.0	121 609 103 18 12.0	
112 612 051 23 19.0	121 609 104 19 13.0	
112 612 052 26 13.0	122 612 011 04 16.0	
112 612 053 18 08.5	122 612 012 11 12.5	
112 612 054 16 08.0	122 612 013 08 08.0	
113 623 011 16 14.0	122 612 014 04 07.0	
113 623 012 09 12.0	122 612 021 08 10.5	
113 623 013 11 21.0		

9.2

211 603 011 23 12.0	212 617 031 31 09.0	221 604 082 07 04.5
211 603 012 10 05.0	212 617 032 25 12.0	221 604 083 04 04.5
211 603 013 16 12.0	212 617 033 27 08.0	221 604 084 27 09.5
211 603 014 07 03.5	212 617 034 16 12.0	221 604 091 25 09.0
211 603 021 32 13.0	212 617 041 15 15.0	221 604 092 22 07.0
211 603 022 15 05.5	212 617 042 23 17.0	221 604 093 26 10.0
211 603 023 21 08.0	212 617 043 18 12.0	221 604 094 21 07.0
211 603 024 47 11.0	212 617 044 11 11.0	221 604 101 21 10.0
211 603 031 09 10.0	212 617 051 06 06.5	221 604 102 07 06.0
211 603 032 07 08.0	212 617 052 16 12.0	221 604 103 07 09.0
211 603 033 14 09.0	212 617 053 19 14.0	221 604 104 10 06.0
211 603 034 06 08.0	212 617 054 11 05.5	222 617 011 12 06.0
211 603 041 30 07.0	213 619 011 23 10.0	222 617 012 07 06.5
211 603 042 31 08.0	213 619 012 10 12.0	222 617 013 14 12.0
211 603 043 26 04.5	213 619 013 19 16.0	222 617 014 10 07.5
211 603 044 31 09.0	213 619 014 30 20.0	222 617 021 08 07.0
211 603 051 34 10.0	213 619 021 23 15.5	222 617 022 07 07.5
211 603 052 11 03.5	213 619 022 23 10.5	222 617 023 10 09.0
211 603 053 12 06.5	213 619 023 14 10.0	222 617 024 05 09.0
211 603 054 32 18.0	213 619 024 17 08.0	222 617 031 16 12.0
211 603 061 35 09.0	213 619 031 20 18.0	222 617 032 04 07.0
211 603 062 38 06.0	213 619 032 23 17.0	222 617 033 08 09.0
211 603 063 43 08.0	213 619 033 07 12.0	222 617 034 19 10.0
211 603 064 50 13.0	213 619 034 09 17.0	222 617 041 26 18.0
211 603 071 49 11.0	213 619 041 25 13.0	222 617 042 29 19.0
211 603 072 32 12.0	213 619 042 19 19.0	222 617 043 29 09.5
211 603 073 14 03.5	213 619 043 06 07.0	222 617 044 12 10.0
211 603 074 28 07.0	213 619 044 12 16.0	222 617 051 16 16.0
211 603 081 19 11.0	213 619 051 16 09.0	222 617 052 11 09.0
211 603 082 20 11.0	213 619 052 16 12.0	222 617 053 10 12.0
211 603 083 31 13.0	213 619 053 30 17.0	222 617 054 17 08.0
211 603 084 16 07.0	213 619 054 21 14.0	223 619 011 24 20.0
211 603 091 17 10.0	221 604 011 22 08.0	223 619 012 09 12.0
211 603 092 44 12.0	221 604 012 03 05.0	223 619 013 19 12.0
211 603 093 20 11.0	221 604 013 14 09.5	223 619 014 10 12.0
211 603 094 28 09.0	221 604 014 04 07.0	223 619 021 15 17.0
211 603 101 09 07.0	221 604 021 03 04.0	223 619 022 19 06.5
211 603 102 40 12.5	221 604 022 06 08.0	223 619 023 10 08.5
211 603 103 11 11.0	221 604 023 07 10.0	223 619 024 19 13.0
211 603 104 09 09.0	221 604 024 06 16.0	223 619 031 31 20.0
212 617 011 38 13.0	221 604 031 16 07.5	223 619 032 14 16.0
212 617 012 65 18.5	221 604 032 14 08.0	223 619 033 33 09.0
212 617 013 31 14.0	221 604 033 03 08.0	223 619 034 17 16.0
212 617 014 31 17.0	221 604 034 23 14.0	223 619 041 19 08.0
212 617 021 35 16.0	221 604 041 12 11.5	223 619 042 10 15.0
212 617 022 28 09.0	221 604 042 10 06.0	223 619 043 02 08.0
212 617 023 14 06.0	221 604 043 17 15.0	223 619 044 12 07.0
212 617 024 25 16.0	221 604 044 06 05.0	223 619 051 07 10.0
	221 604 051 13 11.0	223 619 052 11 15.0
	221 604 052 09 04.0	223 619 053 21 16.0
	221 604 053 18 14.5	223 619 054 22 17.0
	221 604 054 03 07.5	
	221 604 061 50 12.0	
	221 604 062 31 14.0	
	221 604 063 50 12.0	
	221 604 064 99 17.0	
	221 604 071 05 06.0	
	221 604 072 08 07.5	
	221 604 073 21 15.0	
	221 604 074 21 12.0	
	221 604 081 21 12.0	

9.2

311 605 011 07 07.0	313 618 014 12 12.5	322 611 021 21 18.5
311 605 012 16 10.0	313 618 021 07 08.5	322 611 022 08 09.0
311 605 013 14 13.0	313 618 022 11 06.0	322 611 023 07 08.0
311 605 014 21 13.5	313 618 023 26 08.0	322 611 024 07 11.0
311 605 021 30 11.5	313 618 024 26 07.5	322 611 031 13 12.0
311 605 022 22 14.5	313 618 031 20 18.0	322 611 032 13 15.0
311 605 023 07 05.5	313 618 032 03 09.0	322 611 033 11 09.0
311 605 024 12 13.0	313 618 033 08 08.5	322 611 034 15 16.0
311 605 031 23 09.0	313 618 034 07 07.0	322 611 041 23 28.0
311 605 032 20 08.0	313 618 041 17 09.0	322 611 042 05 12.0
311 605 033 26 09.0	313 618 042 23 12.0	322 611 043 11 11.0
311 605 034 45 12.0	313 618 043 20 09.0	322 611 044 11 09.0
311 605 041 17 05.0	313 618 044 07 10.0	322 611 051 10 09.0
311 605 042 34 12.0	313 618 051 26 15.0	322 611 052 09 11.5
311 605 043 22 10.0	313 618 052 17 14.0	322 611 053 10 08.0
311 605 044 15 06.0	313 618 053 12 18.0	322 611 054 14 13.0
311 605 051 30 07.0	313 618 054 17 12.0	323 618 011 13 18.0
311 605 052 33 07.5	321 605 011 06 06.5	323 618 012 16 12.0
311 605 053 18 13.0	321 605 012 12 08.5	323 618 013 28 15.0
311 605 054 17 08.5	321 605 013 09 04.5	323 618 014 16 13.0
311 605 061 36 15.0	321 605 014 13 11.0	323 618 021 16 12.0
311 605 062 24 06.5	321 605 021 23 10.0	323 618 022 10 10.0
311 605 063 31 10.0	321 605 022 10 06.5	323 618 023 09 08.0
311 605 064 33 11.0	321 605 023 16 09.0	323 618 024 09 11.0
311 605 071 19 12.0	321 605 024 11 15.0	323 618 031 05 12.0
311 605 072 08 06.0	321 605 031 10 10.0	323 618 032 06 07.5
311 605 073 26 12.0	321 605 032 09 10.5	323 618 033 14 13.0
311 605 074 23 20.0	321 605 033 12 09.0	323 618 034 08 15.0
311 605 081 09 12.0	321 605 034 13 10.0	323 618 041 08 21.0
311 605 082 14 10.5	321 606 041 11 10.5	323 618 042 05 10.0
311 605 083 07 10.0	321 606 042 09 15.0	323 618 043 10 18.5
311 605 084 13 12.0	321 606 043 06 15.0	323 618 044 02 22.0
311 605 091 18 15.5	321 606 044 08 13.0	323 618 051 07 16.5
311 605 092 11 07.0	321 606 051 08 09.0	323 618 052 09 17.0
311 605 093 21 09.5	321 606 052 07 11.0	323 618 053 05 15.0
311 605 094 13 08.5	321 606 053 07 06.5	323 618 054 07 15.5
311 605 101 06 04.0	321 606 054 02 05.5	
311 605 102 07 05.0	321 606 061 27 15.0	
311 605 103 08 15.0	321 606 062 13 10.5	
311 605 104 13 12.0	321 606 063 13 08.5	
312 611 011 17 08.0	321 606 064 13 12.0	
312 611 012 14 10.5	321 606 071 06 13.0	
312 611 013 17 08.5	321 606 072 13 10.0	
312 611 014 12 12.0	321 606 073 12 10.5	
312 611 021 22 17.0	321 606 074 06 09.0	
312 611 022 11 08.5	321 606 081 04 16.0	
312 611 023 12 07.0	321 606 082 07 12.0	
312 611 024 08 11.5	321 606 083 07 15.0	
312 611 031 15 14.0	321 606 084 05 08.0	
312 611 032 08 13.5	321 606 091 03 10.5	
312 611 033 05 08.0	321 606 092 09 11.0	
312 611 034 04 12.0	321 606 093 03 07.0	
312 611 041 12 16.0	321 606 094 08 14.0	
312 611 042 10 12.0	321 606 101 03 05.0	
312 611 043 07 15.0	321 606 102 04 11.0	
312 611 044 16 18.0	321 606 103 08 07.0	
312 611 051 22 15.5	321 606 104 05 05.0	
312 611 052 16 09.0	322 611 011 03 13.0	
312 611 053 17 06.0	322 611 012 07 07.0	
312 611 054 29 11.5	322 611 013 07 09.0	
313 618 011 08 09.0	322 611 014 17 08.5	
313 618 012 16 12.0		
313 618 013 11 14.0		

9.3

11101	1	18	10	11	2	0	04	1	1	15	04	01	1	12102	2	09	32	04	1	0	03	0	0	10	05	03	2
11101	2	12	22	04	0	0	01	2	1	05	02	01	0	12102	3	25	22	09	0	2	05	0	0	14	04	03	0
11101	3	12	22	11	2	0	00	2	1	16	04	02	1	12102	4	12	22	04	0	1	03	0	0	08	03	01	2
11101	4	16	21	05	0	2	02	1	1	10	03	01	2	12103	1	16	21	05	0	0	09	1	1	11	06	06	0
11102	1	22	33	09	1	0	03	0	0	11	02	01	0	12103	2	24	21	07	1	1	06	0	0	12	03	03	0
11102	2	10	33	03	1	1	01	0	0	05	01	00	0	12103	3	10	21	02	2	1	01	0	0	03	01	00	0
11102	3	09	43	04	2	0	01	0	0	07	01	01	0	12103	4	16	21	04	1	0	03	0	0	06	01	01	0
11102	4	24	22	05	1	1	03	0	0	07	00	00	0	12104	1	16	23	05	1	0	00	2	0	07	02	01	0
11103	1	14	10	06	5	1	01	1	0	13	01	00	0	12104	2	12	22	03	2	0	02	1	0	06	01	01	0
11103	2	12	11	04	2	0	03	0	0	06	00	00	0	12104	3	13	23	02	1	0	01	1	0	04	01	01	0
11103	3	21	10	04	1	0	03	1	0	05	00	00	0	12104	4	10	24	02	0	0	01	0	1	03	02	00	1
11103	4	20	10	03	0	0	04	0	1	08	05	04	1	12105	1	20	04	06	0	0	00	0	1	06	00	00	0
11104	1	15	11	04	2	2	02	2	0	09	01	01	0	12105	2	16	02	03	0	0	03	0	0	06	04	02	1
11104	2	21	11	07	5	1	05	1	0	14	01	01	0	12105	3	12	12	05	0	0	02	0	0	06	03	01	0
11104	3	17	00	09	3	1	07	2	0	20	08	06	1	12105	4	16	12	02	4	0	06	1	1	09	03	03	0
11104	4	21	01	07	2	1	05	4	0	12	02	00	2	12106	1	05	24	02	0	0	00	0	0	02	01	00	0
11105	1	12	12	09	2	0	00	1	1	11	03	00	0	12106	2	12	23	00	0	0	00	0	0	00	00	00	0
11105	2	12	21	01	3	0	02	0	0	06	02	00	0	12106	3	06	34	02	0	0	00	1	0	02	00	00	0
11105	3	14	20	13	6	1	03	1	0	20	00	00	0	12106	4	10	43	00	0	1	00	0	0	01	00	00	0
11105	4	15	21	07	1	0	00	1	1	08	00	00	0	12107	1	12	24	05	4	1	03	0	0	13	03	00	3
11106	1	11	12	01	2	0	03	2	0	04	01	01	0	12107	2	06	24	00	0	0	00	2	0	01	01	00	1
11106	2																										

21101	1	16	32	11	2	3	00	0	0	18	03	00	2	22101	2	10	24	04	1	1	02	3	1	06	02	00	0
21101	2	15	22	11	4	5	02	2	1	22	02	02	0	22101	3	13	24	10	2	0	00	2	1	13	02	01	0
21101	3	13	22	10	2	3	01	3	0	18	04	01	2	22101	4	12	24	02	0	0	00	0	0	03	01	00	1
21101	4	12	32	04	2	6	00	0	1	13	01	01	0	22102	1	06	22	03	0	1	01	0	0	05	02	01	0
21102	1	13	22	07	0	7	04	0	0	19	06	05	0	22102	2	16	10	08	3	2	01	1	0	15	04	01	1
21102	2	09	22	02	0	3	01	0	0	06	01	01	0	22102	3	09	13	01	0	0	00	1	0	02	01	00	1
21102	3	16	12	07	5	2	00	2	0	15	01	00	1	22102	4	12	12	04	0	2	01	0	2	08	02	02	0
21102	4	12	23	00	0	3	01	0	0	05	02	01	1	22103	1	16	24	06	1	2	00	3	1	09	00	00	0
21103	1	13	10	02	0	2	01	0	0	05	01	01	0	22103	2	16	24	04	2	1	00	2	0	08	02	01	0
21103	2	18	10	03	2	2	02	0	0	09	03	01	1	22103	3	12	24	03	0	2	01	1	0	06	01	01	0
21103	3	09	10	03	2	2	02	0	0	09	02	02	0	22103	4	12	14	03	1	2	00	3	1	07	01	01	0
21103	4	11	21	02	0	1	01	0	0	04	01	01	0	22104	1	16	23	17	2	2	00	3	0	24	04	02	1
21104	1	17	12	02	0	3	02	1	0	07	02	02	0	22104	2	17	14	02	1	1	02	2	0	07	03	02	1
21104	2	11	12	03	1	0	01	0	0	06	02	01	1	22104	3	13	24	12	3	1	01	2	0	16	00	00	0
21104	3	18	22	02	0	2	01	4	0	05	01	01	0	22104	4	16	24	09	1	2	02	5	1	14	05	02	0
21104	4	15	22	07	2	1	00	2	1	10	00	00	0	22105	1	16	23	03	1	2	00	1	0	06	01	00	0
21105	1	20	22	04	0	3	00	0	0	07	02	00	0	22105	2	16	23	00	0	0	00	0	0	00	00	00	0
21105	2	13	33	05	0	2	03	0	0	08	02	02	0	22105	3	16	22	07	2	0	01	0	0	09	01	00	0
21105	3	12	21	01	3	1	01	0	0	05	00	00	0	22105	4	14	01	08	0	0	01	0	1	11	04	03	0
21105	4	20	21	04	0	1	04	1	0	08	03	03	0	22106	1	24	13	12	2	3	01	4	2	20	04	02	1
21106	1	27	12	05	2	4	03	0	0	15	06	03	0	22106	2	19	02	11	1	1	02	1	0	15	05	02	0
21106	2																										

1

31101	1	18	11	06	2	1	13	0	0	23	15	11	2	32101	4	12	21	06	1	0	01	0	0	08	02	00	1
31101	2	20	31	07	1	1	05	0	1	19	13	07	3	32102	1	12	33	00	0	0	01	0	0	00	00	00	0
31101	3	12	10	06	0	1	03	1	1	12	06	02	3	32102	2	35	33	07	0	3	01	1	0	12	03	01	1
31101	4	40	20	11	2	1	05	5	2	25	12	07	4	32102	3	15	33	02	0	1	01	0	0	05	02	01	0
31102	1	12	23	02	0	1	01	3	0	06	04	03	1	32102	4	16	11	01	0	0	01	0	0	03	02	02	0
31102	2	12	10	01	0	1	06	0	0	09	08	05	2	32103	1	23	11	03	0	0	00	3	0	03	01	00	0
31102	3	12	12	03	0	0	05	1	0	09	08	05	1	32103	2	35	10	06	0	0	00	2	0	06	00	00	0
31102	4	15	10	02	0	1	05	3	0	09	06	05	1	32103	3	28	21	01	0	0	00	0	0	03	01	00	1
31103	1	09	22	03	2	1	04	0	0	10	04	04	0	32103	4	12	20	04	1	5	00	0	1	09	01	01	0
31103	2	15	01	05	0	1	04	3	0	10	04	03	1	32104	1	21	21	03	0	1	01	0	0	05	02	01	0
31103	3	15	02	01	0	0	02	0	0	05	04	02	2	32104	2	11	20	00	0	1	00	1	0	01	00	00	0
31103	4	31	22	07	1	0	03	2	0	12	05	02	2	32104	3	20	21	00	0	0	01	0	0	01	01	01	0
31104	1	14	10	00	0	1	03	1	0	04	03	03	0	32104	4	12	21	02	0	0	00	0	0	02	00	00	0
31104	2	09	12	01	1	0	03	0	1	03	01	01	0	32105	1	21	21	01	0	0	01	1	0	02	01	01	0
31104	3	11	10	01	0	1	02	0	0	04	02	02	0	32105	2	17	11	03	2	0	00	1	1	05	01	00	0
31104	4	23	11	05	0	0	02	4	0	08	04	02	1	32105	3	20	20	06	2	1	01	3	2	10	04	00	1
31105	1	12	11	02	0	0	01	1	0	02	01	01	0	32105	4	12	20	03	0	0	00	0	0	03	00	00	0
31105	2	35	03	05	3	3	03	3	0	17	06	05	1	32106	1	47	30	13	2	2	04	0	2	22	10	03	2
31105	3	14	00	08	0	3	03	2	0	16	06	04	1	32106	2	09	32	03	0	0	04	1	0	03	02	00	0
31105	4	09	23	06	2	0	00	0	1	16	10	05	3	32106	3	23	32	03	1	0	02	1	0	07	03	01	2
31106	1	15	14	02	0	0	00	3	0	02	00	00	0	32106	4	10	21	02	0	0	05	0	0	06	04	03	1
31106	2																										

APPENDIX 10

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1982-4

Title of thesis or dissertation (or other research projects):

Studies Related to the Concept of Pest - Crop System Design:

- 1) Adult Parasitoid Activity and Its Relation to Biocontrol and
- 2) Forest Harvesting and the Spruce Budworm

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name (s) (typed)

Jan Peter Nyrop

Date 11-13-82

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original: Include as Appendix 10 in ribbon copy of thesis or dissertation.

Copies: Included as Appendix 10 in copies of thesis or dissertation. Museum(s) files. Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

APPENDIX 10.1

Voucher Specimen Data

Page 1 of 1 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of:							
		Museum where deposited	Other	Adults ♀	Adults ♂	Pupae	Nymphs	Larvae	Eggs
<u>Glypta fumiferanae</u> (Vierick)	♀ Delta Co., MI T21N R23W Sec14 caught in malaise traps located in balsam fir trees 7-5-81 Jan P. Nyrop ♂ Delta Co., MI T21N R23W Sec14 caught in malaise traps located in balsam fir trees 7-13-81 Jan P. Nyrop	Entomology Department Michigan State University		10	10				

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Jan Peter Nyrop

Voucher No. 1982-4

Received the above listed specimens for deposit in the Michigan State University

Entomology Museum



Curator

Date

Oct 18, 1983

Date 10-18-82

LITERATURE CITED

LITERATURE CITED

- Barfield, C. S., D. G. Bottrell, and J. W. Smith, Jr. 1977. Influence of temperature on oviposition and adult longevity of Bracon mellitor reared on Boll Weevils. *Environ. Entomol.* 6:133-137.
- Batzer, H. O. and D.T. Jennings. 1980. Numerical analysis of a jack pine budworm outbreak in various densities of jack pine. *Environ. Entomol.* 9:514-524.
- Beck, M. B. 1981. Hard or soft environmental systems? *Ecol. Modeling.* 11:233-251.
- Beddington, J. R., C. A. Free, and J. H. Lawton. 1975. Dynamic complexity in predator prey models framed in difference equations. *Nature.* 225:58-60.
- Beddington, J. R., C. A. Free, and J. H. Lawton. 1976. Concepts of stability and resilience in predator-prey models. *J. Anim. Ecol.* 45:791-816.
- Beddington, J. R., C. A. Free, and J. H. Lawton. 1978. Characteristics of successful natural enemies in models of biological control of insect pests. *Nature.* 273:513-519.
- Berryman, A. A. 1978. Towards a theory of insect epidemiology. *Res. Pop. Ecol.* 19:181-196.
- Berryman, A. A. 1982. Biological control, thresholds, and pest outbreaks. *Environ. Entomol.* 11:544-549.
- Bowman, A. B. 1944. Growth and occurrence of spruce and fir on pulpwood lands in northern Michigan. Michigan State College Agric. Exp. Sta. Tech. Bull. 188 pp.
- Brown, N. R. 1946. Studies on parasites of the spruce budworm, Archips fumiferanae (Clem.) 2. Life history of Glypta fumiferanae (Vierick) (Hymenoptera: Ichneumonidae). *Can. Entomol.* 78:138-147.
- Burnett, T. 1951. Effects of temperature and host density on the rate of increase of an insect parasite. *Amer. Nat.* 85:337-352.
- Burnett, T. 1954. Influences of natural temperatures and controlled host densities on oviposition of an insect parasite. *Physiol. Zool.* 27:239-248.
- Burnett, T. 1956. Effects of natural temperatures on oviposition of various members of an insect parasite (Hymenoptera, Chalcididae, Tenthredinidae). *Ann. Ent. Soc. Am.* 49:55-59.
- Calderon, M. C. 1977. Effect of the nectariless character of cotton on the population dynamics of certain phytophagous and natural enemy insects. Ph. D. dissertation. Dept. of Entomology, Mississippi State University, Mississippi State, Miss. 64 pp.

- Cambell, R. W. and R. J. Sloan. 1977. Natural regulation of innocuous gypsy moth populations. *Environ. Entomol.* 6:315-322.
- Charnov, E. L. 1976. Optimal foraging, the marginal value problem. *J. Theor. Pop. Biol.* 9:129-136.
- Chumakova, B. M. 1960. Complementary feeding as a factor to increase effectiveness of the parasites of injurious insects (Tran. from Russian). *Trans. Inst. Plant. Prot.* 15:57-70.
- Clark, W. C., D. D. Jones, and C. S. Holling. 1979. Lessons for ecological policy design: a case study of ecosystem management. *Ecol. Modeling.* 7:1-53.
- Clark, W. C. and M. Mangel. 1979. Aggregation and fishery dynamics: a theoretical study of schooling and the purse seine tuna fisheries. *Fish. Bull.* 77:317-377.
- Clawson, M. 1977. Decision making in timber production, harvest and marketing. Resources for the Future Research Paper R-4. Resources for the Future, Washington D.C. 127 pp.
- Cook, R. M. and S. F. Hubbard. 1977. Adaptive searching strategies in insect parasites. *J. Anim. Ecol.* 46:115-125.
- Crowly, P. H. 1981. Dispersal and stability of predator-prey interactions. *Am. Nat.* 118:673-701.
- Dowden, P. B., W. B. Buchanan, and V. M. Carolin. 1948. Natural-control factors affecting the spruce budworm. *J. Econ. Entomol.* 41:457-464.
- Gage, S. H., C. A. Miller, and L. J. Mook. 1970. The feeding response of some forest birds to the black-headed budworm. *Can. J. Zool.* 48:359-366.
- Gage, S. H. and C. A. Miller. 1978. A long term bird census in spruce budworm-prone balsam fir habitats in northwestern New Brunswick. *Can. For. Serv. Infor. Rep. M-X-84.* 6 pp.
- Greenbank, D. O. 1963. Host species and the spruce budworm. pp. 219-223. In: *The dynamics of epidemic spruce budworm numbers.* R. F. Morris (ed.). *Entomol. Soc. Can. Mem.* 31:1-332.
- Griffiths, K. J., and C. S. Holling. 1969. A competition submodel for parasites and predators. *Can. Entomol.* 101:785-818.
- Gulland, J. A. 1975. The stability of fish stocks. *J. du Conseil Inter. Explor. Mer.* 37:199-204.
- Hassel, M. P. 1978. The Dynamics of Arthropod Predator-Prey Systems. Princeton University Press, Princeton. 237 pp.

- Hassel, M. P., and R. M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. *J. Anim. Ecol.* 43:567-594.
- Haynes, D. L., R. L. Tummala and T. L. Ellis. 1980. Ecosystem management for pest control. *BioScience* 30:690-696.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91:385-398.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* 4:1-24.
- Hubbard, S. F. and R. M. Cook. 1978. Optimal foraging by parasitoid wasps. *J. Anim. Ecol.* 47:593-604.
- Huffacker, C. B., R. F. Luck, and P. S. Messenger. 1976. The ecological basis of biological control. *Proceedings XV Int. Congr. Entomol.* 560-586.
- Julliet, J. A. 1963. A comparison of four types of traps used for capturing flying insects. *Can. J. Zool.* 41:219-223.
- Kemp, W. P. and G. A. Simmons. 1978. The influence of stand factors on parasitism of spruce budworm eggs by Trichogramma minutum. *Environ. Entomol.* 7:685-688.
- Kemp, W. P. and G. A. Simmons. 1979. The influence of stand factors on survival of early instar spruce budworm. *Environ. Entomol.* 8:993-998.
- Kemp, W. P., J. P. Nyrop, and G. A. Simmons. 1980. Simulation of the effect of stand factors on spruce budworm (Lepidoptera:Tortricidae) larval redistribution. *Great Lakes Entomol.* 13:81-91.
- Keuster, J. L. and J. H. Mize. 1973. Optimization Techniques with Fortran. McGraw-Hill, New York. 500 pp.
- Klomp, H. 1959. Infestations of forest insects and the role of parasites. *Proc. 15th Int. Congr. Zool.* 797-802.
- Lewis, K. 1960. Attractiveness of different foods and flowers to the adults of some hymenopterus parasites. *Can. Entomol.* 92:369-376.
- Lewis, K. 1961a. Influence of various foods on fecundity and longevity of adults of Scambus bioliana (Htg.) (Hymenoptera:Ichneumonidae). *Can. Entomol.* 93:1079-1084.
- Lewis, K. 1961b. Influence of food on fecundity and longevity of adults of Itopectis conquisitor (Say.) (Hymenoptera:Ichneumonidae). *Can. Entomol.* 93:771-780.
- Lewis, K. 1963. Effects of pollens on fecundity and longevity of adult Scambus buoliana (Htg.) (Hymenoptera:Ichneumonidae). *Can. Entomol.* 95:202-207.

- Lewis, K. 1967. Food sources and preferences of adults of a parasite, Scambus buolianae (Hymenoptera:Ichneumonidae), and their consequences. Can. Entomol. 99:865-891.
- Lewis, F. B. 1960. Factors affecting assessment of parasitism by Apanteles fumiferanae (Vier.) and Glypta fumiferanae (Vier.) on spruce budworm larvae. Can. Entomol. 92:881-891.
- Ludwig, D., D. D. Jones, and C. S. Holling. 1978. Qualitative analysis of insect outbreak systems: the spruce budworm and forest. J. Anim. Ecol. 47:315-322.
- MacLean, D. A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: A review and discussion. Forest Chron. 56:213-221.
- Manetsch, T. J. and G. L. Park. 1974. System Analysis and Simulation with Application to Economic and Social Systems Part II. Mich. State Univ., E. Lansing. 239 pp.
- May, R. M. 1976. Simple mathematical models with very complicated dynamics. Nature. 261:459-467.
- May, R. M. 1978. Host-parasitoid systems in patchy environments: A phenomenological model. J. Anim. Ecol. 47:833-843.
- McLeod, J. M. 1979. Discontinuous stability in a sawfly life system and its relevance to pest management strategies. pp. 68-81. In: Current Topics in Forest Entomology, Selected papers from XVth International Congress of Entomology. W. E. Waters (ed.). USDA For. Serv. Gen. Tech. Rep. WO-8. 174 pp.
- Messenger, P. S. 1968. Bioclimatic studies of the aphid parasite Praon exsoletum. Can. Entomol. 100:728-741.
- Miller, C. A. 1958. The measurement of spruce budworm populations and mortality during the first and second instars. Can. J. Zool. 36:409-422.
- Miller, C. A. 1960. The interaction of the spruce budworm, Choristoneura fumiferana (Clem.) and the parasite Glypta fumiferanae (Vier.). Can. Entomol. 92:839-850.
- Miller, C. A. 1975. Spruce budworm: how it lives and what it does. Forest Chron. 51:2-4.
- Miller, C. A., D. O. Greenbank, and E. G. Kettela. 1978. Estimated egg deposition by invading spruce budworm moths (Lepidoptera:Tortricidae). Can. Entomol. 110:609-615.

- Minot, M. C. and D. E. Leonard. 1976. Effect of temperature, humidity, light and gravity on the parasitoid Brachymeria intermedia. Environ. Entomol. 5:427-430.
- Morris, R. F. (ed.) 1963. The dynamics of epidemic spruce budworm populations. Mem. Ent. Soc. Can. No. 31. 322 pp.
- Morrison, G. R. and D. R. Strong, Jr. 1980. Spatial variations in host density and intensity of parasitism: some empirical examples. Environ. Entomol. 9:149-152.
- Munster-Swendsen, M. 1980. The distribution in time and space of parasitism in Epinotia tedella (Cl.) (Lepidoptera:Tortricidae). Ecol. Entomol. 5:373-383.
- Munster-Swendsen, M. 1982. Interactions within a one-host-two-parasitoid system, studies by simulations of spatial patterning. J. Anim. Ecol. 51:97-110.
- Munster-Swendsen, M. and G. Nachman. 1978. Asynchrony in insect host-parasite interaction and its affect on stability, studies by a simulation model. J. Anim. Ecol. 47:159-171.
- Murdoch, W. W. and A. Oaten. 1975. Predation and population stability. Adv. Ecol. Res. 9:2-131.
- Nachman, G. 1981. A simulation model of spatial heterogeneity and non-random search in an insect host-parasitoid system. J. Anim. Ecol. 50:27-47.
- Noy-Meir, I. 1975. Stability of grazing systems: an application of predator-prey graphs. J. Ecol. 63:459-481.
- Parker, G. A. and R. A. Stuart. 1976. Animal behavior as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. Amer. Nat. 110:1055-1076.
- Price, P. W. 1971. A comparison of four methods for sampling adult populations of cocoon parasitoids (Hymenoptera:Ichneumonidae). Can. J. Zool. 49:513-521.
- Peterman, R. M., W. C. Clark, and C. S. Holling. 1979. The dynamics of resilience: shifting stability domains in fish and insect systems. pp. 321-341. In: Population Dynamics the 20th Symposium of the British Ecological Society. R. M. Anderson, B. D. Turner, and L. R. Taylor (eds.). Blackwell, Oxford. 434 pp.
- Pugh, A. L. 1963. DYNAMO's User's Manual. MIT Press, Cambridge. 332 pp.

- Pyke, G. H., H. R. Pullman, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biol.* 52:137-154.
- Real, L. A. 1977. The kinetics of functional response. *Am. Nat.* 11:289-300.
- Reardon, R., W. Metterhouse, and R. Balaam. 1977. Traps for collecting adult parasites of the gypsy moth. *J. Econ. Entomol.* 70:247-249.
- Ricker, W. E. 1954. Stock and recruitment. *J. Fish. Res. Bd. Can.* 11:559-623.
- Royama, T. 1970. Evolutionary significance of predator's response to local differences in prey density: A theoretical study. *Proc. Adv. Inst. Dynamics Numbers Popul. (Oosterbeek, 1970).* 344-347.
- Royama, T. 1971. A comparative study of models of predation and parasitism. *Res. Popul. Ecol. (Suppl. 1):*1-91.
- Royama, T. 1977. Population persistence and density dependence. *Ecol. Mon.* 47:1-35.
- Shahjahan, M. 1974. Erigon flowers as a food and attractive odor source for Peristenus pseudopallipes, a braconid parasitoid of the tarnished plant bug. *Environ. Entomol.* 3:69-72.
- Simmons, G. A., D. E. Leonard, and C. W. Chen. 1975. Influence of tree species density and composition on parasitism of the spruce budworm, Choristoneura fumiferanae (Chem.). *Environ. Entomol.* 4:832-836.
- Southwood, T. R. E. and H. M. Commins. 1976. A synoptic population model. *J. Anim. Ecol.* 45:949-965.
- Syme, P. D. 1966. The effect of wild carrot on a common parasite of the European pine shoot moth. *Can. Dept. For., Bi-mon. Res. Notes.* 20(4):3.
- Syme, P. D. 1975. The effects of flowers on the longevity and fecundity of two native parasites of the European pine shoot moth in Ontario. *Environ. Entomol.* 4:337-346.
- Takahashi, F. 1964. Reproduction curve with two equilibrium points: a consideration on the fluctuation of insect populations. *Res. Popul. Ecol.* 6:28-36.
- Thorpe, W. H. and H. B. Caudel. 1938. Study of the olfactory responses of insect parasites to the food plant of their host. *Parasitology.* 30:523-528.
- Ticehurst, M., and R. Reardon. 1977. Malaise trap: a comparison of two models for collecting the adult stage of gypsy moth parasites. *Melsheimer Entomol. Ser.* 23:17-19.

- Titterington, R. W., H. S. Crawford, and B. N. Burgason. 1979. Songbird responses to commercial clear-cutting in Maine spruce-fir forest. *J. Wildl. Manage.* 43:602-609.
- Townes, H. 1958. Some biological characters of Ichneumonidae (Hymenoptera) in relation to biological control. *J. Econ. Entomol.* 51:650-652.
- Tummala, R. L. and D. L. Haynes. 1977. On-line pest management systems. *Environ. Entomol.* 6:339-348.
- Waage, J. K. 1979. Foraging for patchily distributed hosts by the parasitoid Nemeritis canescens. *J. Anim. Ecol.* 48:353-371.
- Weseloh, R. M. 1976. Behavior of forest insect parasitoids. pp. 99-110. In: Perspectives in Forest Entomology. J. Anderson and H. Kaya (eds.). Academic Press, N. Y.
- Wickham, D. E. and L. W. Botsford. 1980. Multiple equilibria in the interaction between Carcinonemertes errans and its host, the Dungeness crab. *J. Anim. Ecol.*
- Wilkes, A., H. C. Coppel, and W. G. Mathers. 1948. Notes on the insect parasites of the spruce budworm, Choristoneura fumiferanae (Clem.), in British Columbia. *Can. Entomol.* 80:138-155.
- Young, P. 1978. General theory of modeling for badly defined systems. pp. 103-133. In: Modeling, Identification and Control in Environmental Systems. Vansteenkiste (ed.). IFIP, North-Holland.