THE INTEGRATION OF ADULT SURVIVAL AND DISPERSAL INTO A MATHEMATICAL MODEL FOR THE ABUNDANCE OF THE CEREAL LEAF BEETLE, Oulema melanopus (L.)

> Thesis for the Degree of Ph. D. MICHIGAN STATE UNIVERSITY WILLIAM G. RUESINK 1972



This is to certify that the

thesis entitled

THE INTEGRATION OF ADULT SURVIVAL AND DISPERSAL INTO A MATHEMATICAL MODEL FOR THE ABUNDANCE OF THE CEREAL LEAF BEETLE, <u>Oulema melanopus</u> (L.) presented by

William G. Ruesink

has been accepted towards fulfillment of the requirements for

. .

Ph.D. degree in Entomology

Date 3/17/72

O-7639

ABSTRACT

THE INTEGRATION OF ADULT SURVIVAL AND DISPERSAL INTO A MATHEMATICAL MODEL FOR THE ABUNDANCE OF THE CEREAL LEAF BEETLE, Oulema melanopus (L.)

By

William G. Ruesink

The main objective was to develop and analyse a systems model for the population dynamics of the cereal leaf beetle, <u>Oulema melanopus</u> (L.). Numerical values for the parameters were, in general, taken from the literature; however, nothing was available on the mortality rate for the adult beetle nor for the time varying spatial distribution of adults among the various habitats. Consequently, field work was designed and executed to investigate these features.

The resulting model has as components the life stages of the insect: egg, 4 larval instars, pupa, and 3 somewhat arbitrary subdivisions of the adult stage (summer, overwintering, and spring). The internal structure of each component is essentially an accounting of the number of individuals moving in and out together with a time lag ("developmental time") that is a function of environmental temperature.

Analysis of the model revealed its response to a variety of stimuli, one of the most interesting being fluctuating temperatures. For example, rapid buildup of the beetle population is favored by cool springs, especially when there is a large difference between day and night temperatures. Hence the predicted buildup rate for Alpena, Michigan is about twice as great as for Lexington, Kentucky. A second type of response is caused by the differences in temperature between days. Acting through the oviposition rate and developmental times, this fluctuation causes large day to day differences in larval density; changes of up to 20% in a single day are common.

The mortality rate for adult beetles was studied in cages and by a regional survey. Although the magnitude of the mortality rate remains in doubt, it appears that the average daily temperature has a major effect on that rate. For the purposes of the model spring adult mortality was taken as 0.2% per degree-day (above the base of 48° F.) prior to May 18 and 0.4% thereafter. Summer adult mortality was taken as 0.05% per degree-day during the feeding period. Overwintering mortality was taken as 50% between the time summer feeding ceases and spring emergence occurs.

Movement of spring adults between habitats was studied using traps to catch the emerging adults followed by a survey of grain fields. Emergence from overwintering sites occurs primarily from 50 to 150 degree-days, which may take up to 25 calendar days. A portion of the emerging population soon moves into winter grains; the remainder apparently move around the environment and await the occurrence of spring grains. Furthermore, it appears that those beetles entering wheat stay there rather than later moving to oats as has been reported in the literature.

Movement of summer adults into overwintering sites was measured primarily by sifting beetles from soil samples using a cotton gin trash mill. Samples taken from August through November indicate that progressively fewer beetles can be found in the top 3 inches of the soil. This, combined with the fact that in August the measured population was comparable to the population measured the following spring, implies that the majority of the beetles probably overwinter deeper than 3 inches in the soil. THE INTEGRATION OF ADULT SURVIVAL AND DISPERSAL INTO A MATHEMATICAL MODEL FOR THE ABUNDANCE OF THE CEREAL LEAF BEETLE, <u>Oulema melanopus</u> (L.)

> By William G. Ruesink

A THESIS

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

DOCTOR OF PHILOSOPHY

Department of Entomology

ACKNOWLEDGEMENTS

Perhaps every student upon graduating feels much as I do about his major professor. Its only natural, I presume, since he is the one person whose professional interests are closest to the student's. Also there is no other faculty member with whom the student has had greater contact.

Dr. Dean L. Haynes has been more than an advisor to me; he has become the standard of quality against which I will compare all other entomologists and their professional efforts. There is no single trait about him that makes me feel this way, instead it is the combination of his insight, imagination, dedication, foresight, preseverence, and humanness. No other single person comes close to having as much influence of my attitude toward the profession of Entomology.

Although my debt to Dr. Haynes is by far the greatest, I also owe special thanks to: Drs. Gordon Guyer, Kenneth Cummins, William Cooper, and Herman Koenig for serving on my guidance committee; Drs. Robert Ruppel, James Webster, Stanley Wellso, and Mr. Richard Connin for sharing information on the biology of the cereal leaf beetle; and Dr. Gerald Park for teaching me the elements of, and whetting my interest in, systems science.

Finally, I wish to acknowledge the help of everyone in the Department of Entomology, because I honestly believe that half of what

ii

I know about practical entomology came not from classes or thesis research, but from personal conversations with individuals in informal situations.

TABLE OF CONTENTS

Page
INTRODUCTION
LITERATURE REVIEW
DESCRIPTION OF THE MODEL
ANALYSIS OF THE MODEL
Refining the model Sensitivity of the model Predictions and interpretations Initial density Portion preferring wheat Available host acreages Temperature distribution Daily temperature fluctuations
METHODS
The study area Overwintering sites Cage studies of adult mortality Population survey
RESULTS
Overwintering sites Rate of emergence from overwintering Cage studies of adult mortality Regional population survey
DISCUSSION
Overwintering sites Adult mortality from survey data Adult migration from wheat to oats
CONCLUSIONS
LITERATURE CITED
APPENDIX

LIST OF TABLES

Table		Page
1.	Mortality Rates for the Immature Stages of the Cereal Leaf Beetle	. 4
2.	Comparison of MOrtalities Measured by Several Authors at a Common Density of About 200 Eggs per Square Foot in Oats	. 5
3.	Days Required for Each Instar to Complete Larval Development at 60°, 70°, and 80° F	. 6
4.	Effect of a .10 Error in Any Particular Survival Esti- mate on the Resulting Deviation of Generation Index (I) from Its Accepted Value of 1.08	. 21
5.	Average Daily Temperatures for April Through August at Selected Locations in the Potential Range of the Cereal Leaf Beetle	. 30
6.	Generation Index (I), Fecundity (F), Summer Adult Survival (S), and the Dates for Spring Adult Emer- gence (SP), Peak Larval Density (PL), and Summer Adult Emergence (SU) as Predicted for 5 Locations	. 31
7.	August 11-18, 1969 Gin Mill Finds by Habitat at Gull Lake	. 40
8.	Late September and Early October 1969 Gin Mill Finds by Habitat at Gull Lake	. 41
9.	October 23 - November 6, 1969 Gin Mill Finds by Habitat at Gull Lake	. 42
10.	Overwintering Mortality in Above Ground Habitats; Gull Lake 1970 - 1971	. 44
11.	Catch in Emergence Traps for Overwintering Adults 1971	. 45
12.	1971 Spring Adult Emergence by Habitat at Gull Lake	. 47

Table 13. 1971 Spring Adult Emergence by Date at Gull Lake 14. Adults Mortality as Computed from the 1970 Cage Study . . . 15. Number of Cereal Leaf Beetles in Grain Fields in the 4 Square Mile Study ARea for 1970 16. Number of Adult Cereal Leaf Beetles in Grain Fields

17.	Spring Adult Mortality as Computed from the 1971	
	Regional Population Survey	63

in the 4 Square Mile Study Area for 1971

49

54

55

LIST OF FIGURES

Figure		Page
1.	Components of the Cereal Leaf Beetle Population Dynamics Model	11
2.	Generalized Internal Structure of a) the Spring Adult Component, and b) All Other Life Stage Components	12
3.	Predicted Influence on the Generation Index of Varying a) the Initial Population Density (D) of Spring Adults, b) the Portion (P) of the Population Pre- ferring Oats Over Wheat, and c) the Portion (R) of the Small Grain Acreage that is Planted to Oats	27
4.	Two Examples of Predicted Day to Day Fluctuations in Larval Densities: a) for Lansing, and b) for Alpena, Michigan	34
5.	Cumulative Emergence from Overwintering Sites at Gull Lake for 1971: a) Over Calendar Date, and b) Over Degree-Days Accumulated Above the Base of 48° F	50
6.	Log-Probability Plot of the 1971 Gull Lake Cumulative Emergence from Overwintering Sites	51
7.	Rate of Emergence from Overwintering Sites at Gull Lake for 1971, Computed from the Observed Cumulative Emergence	52
8.	Pupal Survival in Oats and in Wheat at Gull Lake for 1970	58
9.	Estimated Spring Adult Population in the 4 Square Mile Study Area for 1971	62

INTRODUCTION

Population dynamics is the study of birth, death, migration, and developmental rates. Considerable work has been done on the population dynamics of the cereal leaf beetle, particularly by entomologists at Michigan State University, Purdue University, the Commonwealth Institue for Biological Control in Delemont, Switzerland, and the Canada Department of Agriculture in Harrow, Ontario; all of the pieces fit together to form the total story.

One of the best methods available for tying together many diverse observations is the method of systems modelling and analysis. Within the field of systems science there exist two major approaches. The one uses models that are mathematically tractable and manipulates these models using standard mathematical procedures. Predictions are obtained from the model in concise form: that is, the answer to any question posed comes out as a simple factual statement. The other approach is to build a logically sound but mathematically complex model that can only be analysed by using large computers. Even then results normally require graphical presentation to be comprehensible. Each approach has its advantages, but essentially in the first the modelling is difficult and the analysis simple, while in the second the opposite is true.

In early 1971 entomologists at Michigan State University joined with systems science engineers as part of a National Science Foundation project (GI-20) entitled "The Design and Management of Environmental

Systems". Together they are modelling the life system of the cereal leaf beetle with the goal of designing an effective pest management program to minimize the effect of the beetle on small grain production. The model presented in this thesis was essentially complete before this cooperative effort began, and consequently it served as a prototype for their efforts.

In the process of developing this model of the population dynamics of the cereal leaf beetle, it became clear that certain aspects of the beetle's dynamics were not adequately described and quantified. Field work was undertaken to do the following: 1) quantify the adult mortality rate as it varies throughout the year, 2) describe and quantify the movement of adult beetles between habitats, and 3) quantify the relative use of various habitats as overwintering sites. The results of the field work, although not as definite as one might hope, were adequate to complete the development of the systems model.

LITERATURE REVIEW

Details of the cereal leaf beetle population dynamics are needed for the development of the systems model in the next section; hence all relevant data from the literature are given here.

Oviposition rate has been studied in the field (Helgesen, 1969) and in the laboratory (Yun, 1967). Maximum daily temperature (T) correlates highly with eggs per female per day (E) over the temperature range of 55° to 80° F. The equation E = 0.4 (T-48) fits Helgesen's field data quite well, and at 80° F this equation predicts 13 eggs per female per day, which agrees with laboratory experience (Wellso, personal communication). Helgesen suggests his cages kept direct solar radiation off the beetles and thereby suppressed the oviposition rate.

Mortality rates for the immature stages have been much studied, but the results are normally presented as total mortality for a given life stage during the entire season. Although this is a good start, more insight could be gained from a study which treated mortality per day as it changes during the year. Recent work in Canada has used the latter approach, but data analysis is incomplete to date (Miller, Gage, and Haynes; in press). The most complete study is that of Helgesen and Haynes (in press) which showed density-dependent mortality in the lst instar in oats and the 4th instar in both wheat and oats; all other mortalities are density-independent (Table 1).

		%	mortality*
Life sta	ige	Wheat	Oats
Egg		10	10
Larva lst ins	star	35	46D-85
2nd ins	star	30	30
3rd ins	star	40	40
4th ins	star	34D-31	28D-18
Pupa		30	30

TABLE 1.--Mortality rates for the immature stages of the cereal leaf beetle (adapted from Helgesen and Havnes, in press)

*D is the common logarithm of the total egg input per ft^2 for the year.

Castro (1964) and Shade, et al. (1970) both attribute the coccinellid <u>Coleomegilla maculata</u> (DeGeer) with considerable predation on cereal leaf beetle eggs; Helgesen and Haynes (in press) assumed no predation occurred. Consequently there is disagreement on the distribution of mortality among the life stages (Table 2), but the total mortality measured for the combined immature stages is quite comparable. Yun (1967) reported field data collected by Ruppel that indicated higher pupal mortality than the other two authors, but lower larval mortality; the combined mortality for all of the immature stages is quite comparable to the other authors.

Overwintering mortality has been reported to range from a low of 25% in straw stubble (Burger, personal communication) up to 100% in

exposed sites 4 feet or more above ground level (Castro et al., 1965). An average value under good conditions seems to be 50%; snow cover and winter temperatures are the major factors affecting this value.

Life	stage	Helgesen and Haynes	Shade et al.	Ruppel (in Yun, 1967)
Egg		10	56	50
Larva		82	65	34
lst	instar	21		
2nd	instar	30		
3rd	instar	40		
4th	instar	46		
Pupa		30	48	91
Egg -	larva	84	85	67
Egg -	pupa	89	92	97

TABLE 2.--Comparison of mortalities measured by several authors at a common density of about 200 eggs per square foot in oats

Dickler (1968) reported that full egg development under constant temperatures required 12 days at 60°, 5.5 days at 70°, and 5 days at 80° F. Yun (1967) gave the equation for % development per day (R) as

$$R = .5473 T - 26.864$$

where T is temperature in °F. Dickler's rate is 1.4 times faster than Yun's. Dickler also found that fluctuating temperatures resulted in more rapid development; for example, eggs hatch sooner when temperature

oscillates from 60° to 80° on a 24 hour cycle than they do at a constant 70°, but he was unable to quantify the magnitude of this effect.

Yun (1967) also gave the equation

$$R = .2866T - 13.0896$$

for the % development per day for the larval stage; Helgesen and Haynes (in press) show that each of the 4 larval instars has a comparable developmental time, but their rate (Table 3) is 1.7 times faster than Yun's.

TABLE 3.--Days required for each instar to complete larval development at 60°, 70°, and 80° F (from Helgesen and Haynes, in press)

	Temperature (°F)		
Larval instar	60	70	80
lst	3.81	2.55	1.86
2nd	5.33	2.12	1.71
3rd	3.00	1.87	1.44
4th	3.59	2.00	1.36
Total	16.24	8.53	5.91
% development per day	6.2	11.7	16.9

Field observations reported by Haynes (personal communication) indicate that temperature is not the only important factor affecting the developmental rate of 4th instar larval. If food is scarce, a nearly developed larva can apparently pupate early; also if the ground is hard and dry, pupation seems to be delayed a bit until it rains. Pupal developmental rate as given by Yun (1967) is R = .2628T - 13.4378. Castro (1964) says 11-14 days at 80°F, which agrees well with Yun's results.

The cereal leaf beetle overwinters in almost any well protected site, usually at or near ground level. Castro (1964) found them under the bark of trees and in logs, in folded leaves, in straws on the ground, in the base of leaf sheaths and ears of standing corn, in baled hay, inside farm structures, in kindling wood, and even inside beehives. He found them in field margins, in the borders of wood lots, and deep within wood lots.

Burger (personal communication) has found relatively high densities overwintering in wheat and oats stubble, especially where the stubble field borders on a woodlot or dense fence row to the north and/or east. Manley (personal communication) has found them consistently at about one per square yard in leaf litter deep within woodlots.

Similar overwintering patterns have been reported for other chrysomelid beetles. Dominick (1939, 1971) and Dominick and Wene (1941) report that the Tobacco Flea Beetle is found "along the edge of wooded areas adjoining tobacco fields, along hedgerows, and in grasslands"; many also hibernate in the soil around the remains of tobacco stalks. Emergence from overwintering sites for that species in the spring is spread over a period of 4 to 6 weeks with no well defined peak.

The literature on mathematical models in population dynamics is very extensive. Two quite distinct approaches have been used: 1) keep the model simple and mathematically tractable at the possible expense

of realism, and 2) make the model realistic even though computer simulation may be the only method of analysis able to handle the resulting complexity. The distinction between these two schools of thought is well described by Liegh (1968).

Pielou (1969) reviewed the use of simple models in ecology, and much of what follows comes from her book. All living organisms tend to expand their populations at a rate proportional to their current size, i.e., $\frac{d Nt}{dt} = r Nt$, where Nt = # individuals at time t and r = intrinsic rate of natural increase. Such exponential growth can only occur at low densities where competition and natural enemies do not exert a density dependent effect.

A more realistic equation that applies to a broader range of population densities is the so called Verhulst-Pearl logistic equation: $\frac{d Nt}{dt} = r Nt \left(\frac{K - Nt}{K}\right)$, where K is the carrying capacity or upper limit of Nt. When K is much larger than Nt, this equation predicts the same rate of buildup as does the exponential, but as Nt approaches K the rate of buildup is suppressed so that Nt approaches K asymtotically from below. Considerable effort has been expended searching for experimental verification of this equation; good fits have been reported by Gause (1934) for <u>Paramecium</u>, by Lotka (1925) for <u>Drosophila</u> and a bacteria colony, and by Odum (1963) for a yeast culture. But Smith (1963) with <u>Daphnia</u> experimentally measured $\frac{dNt}{Ndt}$ and found a non-linear relationship between it and Nt, in contrast to the linear prediction of this model. Pielou (1969) states that this may well be the rule rather than the exception; and that the curve fitting methods of Gause, Lotka, and Odum were simply not sensitive enough to detect the deviations from

the model. Her argument is that the Verhulst-Pearl equation is but one of many possibilities for generating a sigmoid curve; hence when an ecologist finds his population grows sigmoidally, he cannot directly conclude that it fits the Verhulst-Pearl model.

Leslie (1945, 1948) proposed using matrix equations to handle age specific birth and death rates and changing age distributions. A considerable body of literature has grown around this approach (see Caswell, 1971) and some authors (e.g., Lefkovitch, 1965) have experimentally verified their models.

All of the above models were at first simply deterministic, that is only central tendencies are predicted. Bailey (1964) and Pielou (1969) treat the stoclastic generalizations, which include in each case a total accounting of probabilities. Biologists have made very little use of these stochastic methods, largely because of their mathematical complexity.

Watt (1961b, 1968, 1970) advocates the use of complex computer simulation models in population dynamics; he has made several attempts to develop models with sufficient realism that management strategies might be tested on his models rather than on natural populations (Watt; 1961a, 1963, 1964). Most of his work, it seems, results in hypothetical examples of control strategies rather than actual evaluation of feasible stratigies; but even this is better than nothing, for his work has given recent stimulus to much concern with the complex model approach. Two examples are: 1) the occurrence of 3 papers on "modeling insect population systems" in Forest Insect Population Dynamics (1969), and 2) the existence of a large National Science Foundation project at MSU on "Design and management of environmental systems" (GI-20).

DESCRIPTION OF THE MODEL

The computer simulation model developed for this thesis uses age specific oviposition, survival, and developmental rates and difference equations to predict daily population densities in each age class from a known number of overwintering adults as a starting point. A considerable number of simplifying assumptions are made regarding the effect of the environment on the beetles populations dynamics; these will be considered in detail after the model is presented.

The mathematical form and logical structure of the model are described in this section; the FORTRAN version and a sample output are included in the appendix.

The components of this model (Figure 1) are the life stages of the cereal leaf beetle and the internal structure of each component (Figure 2) is simply an accounting of transfer-in minus transfer-out. These transfer rates are computed from the above mentioned rates as reported in the literature.

In the case of survival and movement of the adult beetles there were essentially no useable data in the literature, so observations were made in the field to gather the information. The detailed results of these observations are reported later in this thesis, but relevant facts are used as needed in this section.

Emergence of spring adults from overwintering quarters is modeled as an impulse at 100 degree-days accumulated above a base of 48° F;







Figure 2. Generalized Internal Structure of a) the Spring Adult Component, and b) All Other Life Stage Components.

this corresponds to the time when 50% have emerged and is easier to model than a distributed emergence. After a feeding and host finding period of 10 days, oviposition begins at a rate of N eggs per female per day; N = 0.4 T - 18, where T is the maximum daily temperature in °F. Death of the spring adults progresses at a constant 0.7% per degree day.

Egg developmental rates reported by Dickler (in Helgesen, 1969) were consistantly higher than reported by Yun (1967). A compromise value used here is R = 0.65 T - 31.6, where T is mean daily temperature in °F and R is % development per day. Egg mortality was used as 10% by Helegesen in his computations of larval mortality; however, his data averaged 14%. Other authors indicate that 20% to 50% is more reasonable, consequently Helgesen's estimate of 1st instar mortality most likely contains considerable egg mortality. Since I will be using his estimates of larval mortality, I must also use his estimate of egg mortality as the two are computationally inter-related. So in this model egg mortality is a constant 10% during the life stage, although this will cause the model to predict overly large 1st instar densities.

Larval developmental rates reported by Helgesen were considerably greater than reported by Yun. A compromise value used here is R = 0.42T -19.7, where T and R have the same units as for eggs above. Helgesen (1969) and Castro (1964) show that in the laboratory each of the 4 larval instars have nearly identical developmental rates; in this model they are taken as exactly equal for all temperatures. Larval mortalities are used exactly as given in Helgesen and Haynes (1971); total egg density determines the larval mortality rate, and no changes in

rate that may occur as time progresses are considered. Only in the first and fourth instars is there a difference in mortality between wheat and oats; for the first instar in wheat it is a constant 35% and in oats it follows M = 46 D - 85, where M is % mortality and D is the common log of egg input per ft². Second instar mortality is a constant 30%, and third instar a constant 40%. Fourth instar mortality is given by M = 34 D - 31 in wheat and M = 28D - 18 in oats.

Pupal developmental rates are taken from Yun to be R = 0.26 T - 13.4. Pupal mortality is a constant 30%.

Summer adults feed for 2 weeks during which mortality is 0.70% per degree day. They then diapause to overwinter and a constant 50% survive to emerge the following spring.

Dispersal of the adult beetles and between field variance are included in the simulation model by considering a fairly large (but not precisely defined) geographic area containing both wheat and oats. The number of overwintering beetles, the acreages of wheat and of oats, and the portion of the population preferring wheat are set at the beginning of each computer run.

The acreage of wheat is divided into three parts: 25% will contain a low density of beetles, 50% will contain a medium density--9 times higher than the low density, and 25% will contain a high density--9 times higher than the medium density. The oats acreage is similarly divided. This method of distributing the beetles results in the variance in density being related to the mean regional density according to the relationship reported by Ruesink and Haynes (in preparation): $S^2 = 1.77 \ \overline{x}^{-1.93}$. This corresponds to the observed

relationship between the number of individuals per unit area and the combined within and between field variance.

When the adults first emerge from overwintering, the prescribed portion goes immediately into wheat, distributed among the low, medium, and high density parts as described above. The remaining adults are held aside until May 18 when they are distributed among the oats acreage as described. On May 28 all adult beetles still alive in wheat move to oats; on June 15 all adult beetles still alive leave oats.

Oviposition and mortalities operate independently in each of the 6 "fields". Hence in most cases larval mortality will be considerably greater in the high density "fields" than in the others.

The model as described above actually obscures many causal mechinisms that affect the population dynamics of the cereal leaf beetle. Any mortality caused by weather, disease, predation, or parasitism is considered background noise and simply contributes to the error of prediction. Of course, the data used in developing the model was gathered before any of the parasites specifically imported to combat the beetle had become an important factor, so their effect is excluded.

The method of measuring and computing mortality used by Helgesen actually measures roughly from the midpoints of adjacent life stages rather than from their beginnings or ends. If the majority of the mortality occurs late in a life stage, then this method is very acceptable. For the cereal leaf beetle it is assumed in this model that <u>all</u> mortality occurs at the instant molting begins. This seems to be a reasonably workable assumption.

The developmental times are assumed to be precise measures with no variance term. This simplifies the simulation and should have very little effect on the analysis, unless the variance is very large.

ANALYSIS OF THE MODEL

Refining the model

Before the model can be accepted as an accurate description of the population dynamics of the cereal leaf beetle, it must be tested against certain criteria which are predicated by our knowledge of the beetle. The most important of these criteria are as follows:

1. The average female beetle emerging from overwintering lays from 50 to 200 eggs in her lifetime. This range is not precisely known, but Helgesen (1969) reports in his thesis that beetles collected in early spring and held in field cages averaged 56 eggs per female; some eggs had been laid before he removed these beetles from the field to his cages, so this is an underestimate. An upper limit can be obtained by comparing total egg input per square foot to the starting density of adult beetles in the spring. Helgesen (1969) also reported 1,100 eggs at Gull Lake in 1969; unpublished results of adult densities show the peak density when adults first moved into oats was about 8 beetles per square foot. This gives an upper limit of 275 eggs per female if no adult mortality had occurred between emergence from overwintering and moving into oats. Any mortality during this interval would reduce this upper limit. Another source of data is Yun (1967), who reviewed the European literature and found 4 citations reporting from 50 to 150 eggs per female per season.

- 2. The generation index, the ratio of population size in one year to the population size the previous year, should be between 3 and 18 at low beetle densities, and should decrease to 1.0 as beetle density increases to 5-10 spring adults per square foot. This criterion comes from the Cooperative Cereal Leaf Beetle Sweepnet Survey and from field plot data.
- 3. Adults should emerge from overwintering sites in late April, peak larval density should occur in mid-June, and summer adults should emerge from the soil about July 1. These dates represent the average conditions observed at Gull Lake from 1967 to 1971.

The model as described in the previous section did not fully satisfy these three criteria. Two problem areas were recognized: 1) fecundity was somewhat too low (58 eggs per female per season), and 2) summer adult mortality was far too high, 91%, resulting in a generation index less than 1.0 even at low beetle densities. The two changes made to correct these problems are described below together with the reasoning used to arrive at the new parameter values.

In the original model spring adult mortality was 0.7% per degree day. This value came from the 1971 regional survey and was first believed to be the most accurate. But perhaps the value of 0.4% per degree day obtained in the 1970 cage study is better. One reason the 1971 value might be too big is if the insecticide killed more than the number of adults present in the sprayed fields at the time of application. This is expected if there is considerable between field movement of beetles. Also it appears from the data that mortality may be even lower very early in the spring. Hence in the revised version spring adult mortality was used as 0.4% per degree day after May 18 (the date they move into oats) and half this before May 18.

The second change was to reduce summer adult mortality to 0.05% per degree day. This particular value has no base in the data, but was chosen so that total mortality for the summer adults would be between 10 and 20%. There is a reasonable explanation why the cage study would accurately estimate spring adult mortality, yet very much overestimate summer adult mortality. Based on results presented later in this thesis, it seems that the cereal leaf beetle may overwinter fairly deep in the soil. If some of the beetles put into the cages for mortality studies completed their feed-out phase and began digging into the soil to overwinter, then they would not be found during the search for surviving beetles and consequently would be counted among the dead.

These changes caused the simulation model to satisfy all three criteria. Further data are needed to determine if these changes were the proper ones to make, but at least they appear reasonable and result in the model behaving in accordance with the presently known population dynamics of the cereal leaf beetle.

Sensitivity of the model

The next important consideration is the sensitivity of the model to small changes in parameter values. For example, egg mortality is set at .10; what would happen if that were changed to .20? The answers to this type of question are important because they tell us how accurately we should know these values and what the consequences of an error might be.

Perhaps the most important response variable in this model is the generation index (I), which is essentially predicted from the product of fecundity and the age specific survivals:

 $I = F \cdot S_E \cdot S_I \cdot S_2 \cdot S_3 \cdot S_4 \cdot S_p \cdot S_{SA} \cdot S_W$ Of course, in the simulation model this I is computed as the ratio of adults surviving the winters of two subsequent years. But the sensitivity of I to changes in survival and fecundity can just as well be studied via this equation rather than the simulation.

There are at least 3 different ways to view this sensitivity. The simplest is to consider the effect of a multiplicative change in a single variable. For example, suppose fecundity is doubled; the result is a doubling of I. If F is halved, I is halved. This relationship holds for every variable in the equation.

A second approach is to consider the effect of changing survival by .10 for any given variable. Table 4 shows the results at an initial egg density of 1,000 per square foot in oats. Inspection of that table reveals that when survival is high, a .10 error has little affect on I; but when survival is low, a .10 error can cause important changes in the predicted I. This interpretation implies that this model should be more accurate at low densities than it is at high densities.

A third approach to evaluating the sensitivity of I to the survivals is to assume that each survival is known plus or minus its standard error; we can consider the combined effect of all 8 survival terms simultaneously by computing the standard error of I using the standard equation for the product of random variables as given in Yates (1953):

400	Observed	Predicted I if survival is		
Class (i)	value (S _i)	Higher (S ₁ + .10)	Lower (S _i 10)	
Fecundity ^a	56			
Egg	.90	1.20	.96	
lst instar ^b	. 47	1.31	. 85	
2nd instar	.70	1.23	.93	
3rd instar	.60	1.26	.90	
4th instar ^b	. 37	1.37	.79	
Pupa	.70	1.23	.93	
Summer adult	.84	1.21	.94	
Overwintering	.50	1.30	.86	

TABLE 4.--Effect of a .10 error in any particular survival estimate on the resulting deviation of generation index (I) from its accepted value of 1.08

^aFecundity is 56 eggs per beetle or 112 eggs per female. ^bAt a density of 1,000 eggs/sq. foot in oats.

SE (xy) =
$$\sqrt{(Y \cdot SE(x))^2 + (x \cdot SE(y))^2}$$

If the standard error of the estimated survival is .10 for each of the 8 terms, and the standard error of fecundity is 10 eggs, then the calculated standard error for I using the values in Table 4 is .57; hence the generation index may lie anywhere between 0.51 and 1.65. At a lower density, I is computed to lie between 2.85 and 7.27.

This sensitivity of the response variable I to the accuracy of the fecundity and survival estimates is an important consideration. If we wish to use this model to predict the <u>absolute</u> merit of a proposed management strategy, then we would probably want the model to predict I within \pm 20%. The above argument has just shown that fecundity within \pm 10 eggs per beetle and age specific survivals with 0.10 only result in an accuracy for I of about \pm 50%. So considerable accuracy is required of our ability to predict fecundity and survivals.

If, on the other hand, we wish to use the model to evaluate the <u>relative</u> merits of several proposed management strategies, then less accuracy is required. In this case it is sufficient to know that strategy A will produce a larger generation index than strategy B, and therefore strategy B is preferred over A for the control of the cereal leaf beetle.

A second response variable of particular interest is <u>when</u> certain points in the life cycle of the beetle occur. Specifically, when does the spring adult emerge from overwintering, when does peak larval density occur, and when do the new summer adults emerge from the pupae?

The date that adults emerge from overwintering is determined in the model by accumulating degree days above the base 48° F. beginning

April 1. The standard temperature distribution used in the model results in spring adult emergence on April 26; if instead of 100 degreedays we had used 80 or 120, then emergence would have occurred on April 22 or 28 respectively. Since six days in April has very little effect on the resulting egg and larval population, an error of 20 degree days is of little importance.

The developmental rate functions for egg, larva, and pupa can be interpreted as predicting the accumulated degree days above base 48 needed to complete development through those stages; they predict approximately 160,220, and 460 degree days respectively. The following discussion considers only the effects of prolonging developmental times beyond those used in the model, but an analogous argument can be made for the effects of reducing developmental times.

If egg developmental time were 200 degree days instead of 160, this would cause egg hatch to occur 40 degree days later in the season. Consequently peak larval density and summer adult emergence would also occur 40 degree days later, which is 2 days at 68 degrees mean temperature (the average for late June is about 70). So again a relatively large error in estimation of developmental times has very little consequence in the model.

If larval developmental time were 260 degree days instead of 220, and egg developmental time were 160 as before, then egg hatch would occur at the normal time, but pupation and summer adult emergence would be about 2 days later than normal--exactly the same end effect as prolongation of egg developmental rate. However, since 2 extra days are spent in the larval stage, the peak larval density would be somewhat higher than before and would occur about two days later than before.

If pupal developmental time were 500 degree days instead of 460, there would be no effect on eggs or larvae, but summer adult emergence would simply be postponed about 2 days.

Any error of prediction of less than 7 days can probably be tolerated, with the possible exception of when the model is used to evaluate management strategies involving precise timing of insecticide applications. An error of 7 days would only occur if there were an across the board error of over 15% in the estimation of developmental rates.

A third response variable, which is not important for the analyses included in this thesis but is very important in age specific mortality studies and in any work with predation or parasitism, is the size or density at any point in time of each age class. In other words this response measures the model's ability to generate total incidence curves. Since this response is not important in the context of this thesis, it will not be studied in detail, but let it suffice to say that considerable discrepancy is anticipated between observational data and model predictions. There are three basic reasons for this: 1) a 10% error in developmental time will result in a 10% error in the height of the generated incidence curve, 2) since all age specific mortalities are applied at the end of each life stage, the generated incidence curves will always be somewhat higher than they should, and 3) the model does not consider any changes in survival that may occur as time progresses; so if larval survival in May is better than in late June, the observed incidence curves will be peak earlier than predicted and have a shorter late season tail.
Predictions and interpretations

The items covered in this section differ from those of the preceding section in a rather subtle fashion. That section covered the response of the model to changes in certain variables which have observed values--values presumed to be constant over a wide range of space and time. This section considers the model's response to changes in parameters which vary considerably in space and time.

First I should explain the method of analysis used in this section. Four different parameters are studied; each one is considered independently of the others. Except for the one being varied in each case, the others are held constant at what I refer to as its "standard" value. The standards are as follows:

- Population size (CLBN in the program)--1,000,000 spring adults just ready to emerge from overwintering sites.
- Portion of the adult population preferring wheat (RATIO in the program)--.10; that is, 90% of them go into oats the 18th of May.
- Acreage of wheat and of oats available to the beetles--100 acres each.
- 4. Temperature distribution--roughly fits the 30 year mean for Gull Lake and assumes the daily high is always 10° greater than the mean. It should be emphasized in light of the sensitivity analysis in the preceding section that the following interpretations and predictions may lack accuracy in regards to the absolute value of the generation index predicted, but they should be very accurate relative to one another.

<u>Initial density</u>: The starting size of the spring adult population was varied from 10,000 to 100,000,000 which corresponds to .001 and 10 per

square foot of grain respectively. The generation index (I) was at a maximum of 6.0 at the lowest density and stayed there until the density reached about .02; I then began declining, until about 7 beetles per square foot it reached 1.0 (Figure 3a). I continued to decrease, getting close to zero as the initial density became very large.

This is exactly the behavior expected. Helgesen (1969) accurately described this as a density-dependent feedback system, the requisite for population regulation. The biological interpretation is that whenever initial density is less than 7 beetles per square foot, the population will increase; whenever it is greater than this, it will decrease. Hence regardless of what the initial density is, after many generations the density will be close to 7 per square foot.

One point needs emphasis here: not too much importance should be attached to the value 7 per square foot. There are two reasons I say this. First is that the sensitivity analysis showed the model could be about 50% off in predicting the generation index; reconsideration of Figure 3a knowing this shows that I may reach 1.0 at any density between 3 and 18 per square foot. Second is that this 7 is <u>average</u> for the area. Some fields always have more, others less, than the average due to between field variance. The important interpretations here are that population size is density regulated and that density-dependent mortality begins to exhibit its effect on the generation index when regional density is still about 400 times less than the carrying capacity.

Portion preferring wheat: At first it may seem that this parameter should be a constant, somehow determined by the genetic makeup of the beetle population. Or maybe it should even be a constant 0.0, because

Figure 3. Predicted Influence on the Generation Index of Varying a) the Initial Population Density (D) of Spring Adults, b) the Portion (P) of the Population Preferring Oats over Wheat, and c) the Portion (R) of the Small Grain Acreage that is Planted to Oats.



all of the beetles actually prefer oats. But, in fact, this parameter is quite variable and quite important, considerably more so than was thought by most researchers until now.

The response of the generation index to changes in beetle preference is quite small (Figure 3b), only ranging from 5.85 to 4.62 as preference moves from all in wheat to all in oats. And most of this difference is due to the fact that beetles which prefer oats effectively lose part of their potential egg output before May 18 because no host is available for oviposition.

More important is the movement of the spring adult among host plants, a factor not reflected in the response of the generation index. This consideration is of extreme importance if one considers directing control strategies against the adult to prevent oviposition.

<u>Available host acreages</u>: There are two separate issues regarding host acreages: 1) what total acreage of small grains is available in the region, and 2) what portion of that acreage is spring grains. The first, total available acreage, affects density and consequently affects generation index as shown in Figure 3a. The second issue is a bit more interesting.

The ideal habitat, from the point of cereal leaf beetle population buildup, is one that contains both winter and spring grains (Figure 3c). Both pure oats and pure wheat cultures suppress the generation index (I), primarily because fewer eggs are laid when oviposition is restricted to one crop or the other. But I is also suppressed when 99% of the small grain available is one crop and only 1% is the other. In this case the reason is that when so many adults concentrate in a small area,

the resulting high egg and larval density causes an increased larval mortality.

It is interesting to note the interaction between host crop relative acreages and the beetle's inherent preference for oats. If 90% of the beetles prefer oats, I peaks at 5.1 when 90% of the small grain acreage is in oats. If 50% of the beetles prefer oats, then I peaks at 5.45 when 50 to 60% of the small grain acreage is in oats. So it seems that optimal rate of population growth occurs when the proportion of small grain acreage planted to oats corresponds to the proportion of cereal leaf beetles preferring oats.

<u>Temperature distribution</u>: Temperature affects the beetle population three ways in this model: 1) oviposition rate is directly proportional to maximum daily temperature, 2) adult survival is inversely proportional to mean daily temperature, and 3) accumulated degree-days determines when events such as emergence from overwintering and peak larval density occur.

Five different temperature distributions were considered (Table 5), corresponding to the 30 year averages for five geographic locations within the current or anticipated range of the cereal leaf beetle. Lansing and Alpena were chosen because we know something about the beetle's dynamics in these areas. Consequently, the predictions of the model for these two areas can be evaluated with respect to accuracy. The other three areas, Bismark, N. D., Ottawa, Ont., and Louisville, Kty., lie on the periphery of the beetle's current range. Predictions of the beetle's dynamics in these areas will be useful for timing detection surveys and for anticipating the rate of build-ups.

Location		April	May	June	July	August
Bismark,	Ha				86	
N. Dakota	L^{b}				58	
	MC	44	56	65	72	69
Ottawa,	н	50	65	75	80	78
Ontario	L	31	43	53	58	55
	М	40	54	64	69	66
Louisville,	н	66	76	85	89	87
Kentucky	L	43	57	62	67	64
	М	54	66	74	78	76
Alpena,	Н	52	66	76	80	79
Michigan	L	29	39	49	53	53
	М	40	52	62	66	66
Lansing,	Н	56	68	78	83	82
Michigan	L	36	46	56	60	59
	М	46	57	67	72	70

TABLE 5.--Average daily temperatures for April through August at selected locations in the potential range of the cereal leaf beetle

 $^{a}_{H}$ is the average daily high temperature.

^bL is the average daily low temperature.

 $^{\rm C}{\rm M}$ is the average daily mean temperature.

Table 6 presents the summarized results of this analysis. The dates for Lansing and Alpena are as expected, so the other dates are probably close to what would actually occur. The expected north-south gradient is quite evident, except that Bismark compares very closely to Lansing rather than to other more northerly sites; but Table 5 shows that Bismark's temperature distribution is also very much like Lansing's, so comparable dates should be expected.

TABLE 6.--Generation index (I), fecundity (F), summer adult survival (S), and the dates for spring adult emergence (SP), peak larval density (PL), and summer adult emergence (SU) as predicted for 5 locations

				Date				
Location	I	F	S	S P	ΡL	SU		
Bismark, N.D.	6.1	147	. 84	May 3	June 13	July 7		
Ottawa, Ont.	6.6	154	.87	May 9	June 16	July 14		
Louisville, Kty.	3.5	84	.81	Apr 13	May 22	June 15		
Alpena, Mich.	6.9	156	.90	May 10	June 21	July 22		
Lansing, Mich.	5.4	128	.85	Apr 29	June 13	July 7		

A north-south gradient is also evident for generation index, fecundity, and survival of summer adults. Fecundity is highest in the north where, 1) cooler mean daily temperatures cause the ovipositing adults to live longer, and 2) at the same time the day-night temperature fluctuation is greater, so for a given mean temperature the daily maximum is greater than in the south; daily oviposition is determined by the maximum temperature, so more eggs result. Summer adult survival is highest, as expected, in the coolest climate. The combination of increased fecundity and increased survival of summer adults causes the generation index to be highest in areas of cool mean temperatures with large day-night fluctuations.

There are at least three factors not considered that may have important effects on Table 6. One is the influence of relative acreages of winter and spring grains in each region. The present computations were made assuming equal acreages of each, and small deviations from this should have little effect. But in fact North Dakota has essentially no winter grains and Kentucky has essentially no spring grain. Just how the beetle will adapt to these conditions, and what portion of the resulting resident population will prefer spring grain over winter grain remains unknown.

The second factor involves the causal relationships affecting oviposition rates and adult mortality. If these rates are not related to temperature, or if they are related in some fashion considerably different than currently modeled, then fecundity, summer adult survival, and generation index as reported might be far from accurate.

The third factor affects Kentucky and other warm climate areas; emergence from overwintering sites is modeled as occurring at 100 degree-days accumulated after April 1. In the north this works well, but in Kentucky March is warm enough that in fact the beetles may emerge before April even begins. Since this possibility was not considered in construction Table 6, the dates there for Kentucky must be biased toward lateness. If spring adult emergence occurs April 1 rather than April 13, then 1) fecundity would be greater (maybe about 100),

2) generation index would be greater (maybe about 4.2), and 3) both peak larval density and summer adult emergence would occur earlier (maybe 7 days earlier).

Daily temperature fluctuations: If daily temperatures followed the smooth curves obtained from the 30 year means, then the total incidence curves for the immature stages of the beetle would also be very smooth. Instead we have warm and cool days intermixed, which cause egg input and larval developmental times to be irregular. These irregularities in turn cause the total incidence curves to be quite rough. For example, Figure 4 shows the total incidence curves for larvae that the model generated using the temperature distributions at Lansing and Alpena, Michigan. Especially notice the sharp drop in density from day 79 to day 80 on the Alpena curve; in one day density dropped over 35%, then climbed back to nearly its original level before the normal late season decline began.

The following sections of this thesis pertain to the field work that was done to support the model.



Figure 4. Two Examples of Predicted Day to Day Fluctuations in Larval Densities: a) for Lansing, and b) for Alpena, Michigan.

METHODS

The study area

An 1842 acre area in the northeast corner of Kalamazoo County, Michigan was chosen for this study; the majority of that acreage belongs to the Kellogg Biological Station, hence is under control of Michigan State University. For the purposes of estimating the total number of cereal leaf beetles in this region, the 1842 acres were divided into several categories, then density estimates were taken from each category. The 1,315 acres under cultivation was distributed among about 300 fields ranging in size from 0.8 acres to 35.8 acres. The remaining 527 acres was subdivided as follows: woods, 249 acres; fence rows, 13 acres; roadsides, 27 acres; weeds, 25 acres; and others, 213 acres. The final category contains such things as lakes, roads, buildings, and lawns. None of these were sampled as they were considered unavailable to the cereal leaf beetle as habitat.

Overwintering sites

An extensive search was conducted to find the preferred overwintering sites of the cereal leaf beetle. Several methods were used, the principal one being to dig up a sample (roughly 3 square feet and 3 inches deep) of earth including all plants above that area and run it through a cotton gin trash mill. This machine was acquired from the Plant Pest Control division of the U.S. Department of Agriculture; they

had designed and used it to survey for pink bollworm larvae in the trash left from ginning cotton. The machine consists of two revolving screen cylinders which sift the material of the sample into three parts according to particle size.

When the soil was loose and dry, this machine efficiently separated the beetles from the soil and most of the debris. Excessive moisture caused mud to clog the screens, so the beetles were not then separated out.

Especially designed emergence traps were used in the spring of 1971 to sample the number of beetles emerging from overwintering sites. These traps covered a square yard of ground surface and caught emerging insects in a pan of glycol when they reached the top of the screen sides.

Beetles were also found in their overwintering sites by direct observation. Old fence posts were torn apart, bark was stripped from wild grape, and leaf litter was sifted in the field. These latter techniques did reveal some beetles, but in general the gin mill and emergence cages provided the most information.

Cage studies of adult mortality

In 1970 the mortality rate of adults was studied using a field cage technique. The cages used were 6-1/2 feet square and 6 feet high with plastic screening for the sides and top and with a zipper door in one side; the bottoms were open so the cages could be placed over the host plants in the field. Two cages were used for spring adults; the first three weeks they were in wheat, the last two in oats. Four cages were used for summer adults; two in oats and two in corn for the entire three weeks. In every case when a cage was first set up in a new

location, it was necessary to remove the resident beetles before the study began. This was accomplished by a visual search using a hand aspirator to collect every beetle seen. When no more could be found, the person left the cage for about 1/2 hour and then came back and repeated the search. Normally the second search caught about one-tenth as many beetles as the first.

Each week 250 beetles were put into each empty cage. After 6 to 8 days the cages were again emptied using the same search process described above.

When the beetles were introduced into an emptied cage at the start of each trial, the jar containing them was opened and placed inside the cage. Those found dead in the jar when the cage was emptied a week later were subtracted from the number introduced before computing mortality. Hence the % mortality over the sample interval was found from this equation:

	$M = 100 \times \frac{I - D - R}{I - D}$,
where	I = no. put into cage,
	D = no. found dead in jar, and
	R = no. removed 6-8 days later.

Population survey

Each grain field in the study area was sampled to determine the number of beetles in that field; the sum from all fields estimated the number in the region. Every field was sampled at regular intervals, normally twice a week, to detect any change in beetle population. Mortality of adults was computed by comparing the population on successive sample dates.

The sampling technique used varied with crop height. Grain less than 10 inches tall was sampled using a thrown stick technique while taller grain was swept with a 15 inch diameter sweepnet. One sample with the stick technique consisted of: 1) throwing a 12 inch garden stake at least 10 feet from where one stood, 2) moving the stake 2 stake lengths further down the grain row, and 3) counting the beetles in 12 inches of 2 adjacent grain rows. One sample with the sweepnet technique consisted of 10 sweeps each 5 feet long keeping the top rim of the net as close as possible to the top of the grain plant.

Sweepnet catch per sweep (C) was converted to number per square foot (D) by the equation given in Ruesink and Haynes (in preparation):

$D = C (0.20 + 10^{K}),$

where $K = -.06 + .02 H - .017 (T + 10S) + .661 \log_{10}(W + 1)$,

- H = grain height (inches),
- T = temperature (°F),
- S = solar radiation (cal/cm²/sec), and
- W = wind (mph).

Most of the needed weather data were available from our own weather station set up within the study area; however, some data came from U.S. Weather Bureau records for Jackson, Michigan.

RESULTS

Overwintering sites

The gin mill samples taken August 11-18, 1969 found beetles in nearly every habitat surveyed (Table 7); the total estimate of 10,351,000 beetles in the 4 mi² region is reasonably close to the 5 to 10 million expected based on population levels the following spring. By late September and early October, however, less than 1 million could be accounted for by using the gin mill, and by early November only 430,000 were accounted for (Tables 8 and 9). Hence it appears that actual overwintering does not occur in the surface litter nor in the top 3 inches of soil.

Ground litter samples collected March 20, 1970 were held at 65° F in the laboratory; 4 beetles emerged from 72 square feet of straw stubble, 1 from 4 square feet of fence row litter, and none from 4 square feet of an old hay windrow. This accounts for 2,420 per acre in stubble, or 636,000 in the 4 square miles, perhaps 10% at the most of those present in the 4 square miles; the fence rows may account for another 2%, according to these meager data.

Straw stubble was again checked in the late summer and fall of 1970. Beetles were found in 6 of the 9 fields surveyed at an average density of 0.14 per square foot, or 6098 per acre, which is 1.7 million in the 4 mi² area. Three yd^2 litter samples from fence rows gave 15 beetles, or 0.3 million in the 4 mi² area.

Habitat	# CLB	# Samples	# CLB/ # acre acres		Total # CLB (1,000's)				
Croplands									
Idle	3	7	6,222	529	3,291				
Grain Stubble	11	21	7,606	263	2,000				
Alfalfa	1	9	1,613	216	348				
Corn	2	6	4,840	267	1,292				
Subtotal	17	43	1,30		6,931				
		Non-cı	coplands						
Woods	7	12	8,470	250	2,118				
Fence rows	13	6	31,460	13	409				
Roadsides	37	21	25,583	27	691				
Weeds	5	9	8,066	25	202				
Subtotal	62	48		527 ^a	3,420				
Total	79	91		1,830 ^a	10,351				

TABLE	7Augus	t 11-18,	1969 gi	n mill	finds	by habitat	at Gull	Lake.
	Each	sample c	onsisted	of 3	square	feet		

^aIncludes acreage not sampled, but CLB density assumed zero.

Habitat	# CLB	# Samples	<pre># CLB/ acre</pre>	# acres	Total # CLB (1,000's)				
Croplands									
Idle	1	18	807	529	427				
G rain st ubble	0	30	0	263	0				
Alfalfa	0	26	0	216	0				
Corn	1	45	323	267	86				
Subtotal	2	119		1,303 ^a	513				
		Non-cr	coplands						
Woods	1	9	1,613	250	403				
Fence rows	4	23	2,525	13	33				
Roadsides	0	15	0	27	0				
Weeds	0	20	0	25	0				
Subtotal	5	67		527 ^a	436				
Total	7	186		1,830 ^a	949				

TABLE	8Late	September	and	early	October	1969	gin	mill	finds	by
	habit	tat at Gull	L Lal	ke						

^aIncludes acreage not sampled, where CLB density assumed zero.

Habitat	# CLB	# Samples	<pre># CLB/ acre</pre>	# acres	Total # CLB (1,000's)					
Croplands										
Idle	0	9	0	529	0					
Grain stubble	0	3	0	263	0					
Alfalfa	0	12	0	216	0					
Corn	2	18	1,612	267	430					
Subtotal	2	42	1,303 ^a		430					
		Non-cr	coplands							
Woods	0	3	0	250	0					
Fence rows	0	0	(O) E	lst. 13	(0) Est.					
Roadsides	0	4	0	27	0					
Weeds	0	3	0	25	0					
Subtotal	0	10		527 ^a	0					
Total	2	52		1,830 ^a	430					

TABLE 9.--October 23 - November 6, 1969 gin mill finds by habitat at Gull Lake

^aIncludes acreage not sampled, where CLB density assumed zero.

On November 6, 1970 an old weathered fence post was torn apart; 18 live and no dead beetles were found in its cracks and crevices. This was my first sample from such a habitat and indicated that significant numbers of beetles may overwinter in micro-habitats which are very hard to quantify.

In early April of 1971 some more searching was done to find out if large numbers of beetles overwintered in such cracks in logs. Of the 162 beetles found in 4 old fence posts, a decaying stump, and under wild grape bark, only 9 were alive (Table 10). Since these samples were taken before the weather was warm enough for spring emergence to begin, the difference between the observed survival in November and in April represents overwintering mortality. In November 100% of the beetles were alive while in April only 6% were alive, so overwintering mortality in above ground exposed habitats is estimated at 94%.

Of the 32 emergence traps set out in the spring of 1971, 18 caught one or more beetles, 2 were nonfunctional, and 12 others caught nothing. The detailed catches are listed in Table 11, while Table 12 summarizes catch by habitat. These 32 traps were not placed at random in the environment, but were placed in sites where overwintering beetles were expected based on previous gin mill work. Still, by proper stratification of the environment, an estimate of the beetle population can be made as follows: consider 4 beetles in 7 yd² as the average density for all cropland, woods interiors, and the so called weeds. Estimating 20% of the woods acreage as edge and 80% as interior gives us 1528 acres at the above density, or 4,226,000 beetles. The high density area is made up of woods edges, fence rows, and road sides. In this area 109 beetles

		<pre># CLB found in</pre>	April 1971
Habitat		# Dead	# Alive
Fence post	#1	8	0
Fence post	#2	0	0
Fence post	#3	139	7
Fence post	#4	1	1
Decaying stump		0	0
Under wild grape bark		5	0
Totals		153	9
% mortality = $\frac{153}{153 + 9} \times 100\%$	= 94.5%		

TABLE 10.--Overwintering mortality in above ground habitats; Gull Lake 1970 - 1971

TABLE 11.--Catch in emergence traps for overwintering adults 1971

	ТьтоТ	2	н	e	2	65	2	-+	Ч	4	16	4	Ч	7
	6/ 22	ł	ł	0	ł	0	ł	ł	1	0	0	0	0	0
	6/ 17	-	ł	0	ł	0	ł	ł	ł	0	0	0	0	0
	6/ 14	ł	1	0	ł	0	ł	ł	ł	0	0	0	0	0
	6/ 12	ł	1	0	ł	0	ł	ł	1	0	0	0	0	0
	6/	1	ł	0	ł	0	ł	ł	ľ	0	1	0	0	0
	6/ 5	l	ł	0	ł	0	ł	ł	ł	0	0	0	0	0
	6/	1	ł	0	ł	0	ł	ł	ł	0	0	0	0	0
	5/ 29	ł	ł	Ч	ł		ł	ł	1	2	0	0	0	0
te	5/ 22	ł	ł	0	ł	0	ł	ł	ł	0	ς	Ч	0	0
y da	5/ 21	0	0	0	ł	0	0	0	0	0	0	0	0	0
ch b.	5/ 18	0	0	0	ł	0	0	0	0	0	7	0	0	0
Cato	5/ 15	0	0	2	ł	2	0	0	0	0	0	1	0	0
	5/ 10	0	0	0	ł	9	0	0	0	0	1	0	0	0
	5/ 7	0	0	0	ł	9	0	0	0	0	7	2	0	0
	5/	0	0	0	ł	0	0	0	0	1	2	0	0	0
	4/	0	0	0	ł	0	0	0	0	0	0	0	0	0
	4/27	0	0	0	ł	0	0	0	0	0	0	0	0	0
	4/ 23	0	0	0	0	0	0	0	0	0	0	0	0	0
	4/ 21	1	1	0	1	38	2	0	Ч	Ч	0	0	Ч	2
	4/ 18	0	0	0	0	ę	0	0	0	0	0	0	0	0
	4/ 16	1	0	0	Ч	6	0	Ч	0	0	0	0	0	0
F	Date Temovec	5/21	5/21	6/22	4/23	7/15	5/21	5/21	5/21	6/22	6/22	6/22	6/22	6/22
ца	Date se	4/2	4/2	4/2	4/2	4/2	4/2	4/8	4/8	4/13	4/13	4/13	4/13	4/13
E	* qeiT	2	с	4	2	7	6	13	16	19	20	22	23	24

e	9	٦	ı	2	117
0	0	0		ł	0
0	0	0	ł	ł	0
0	0	0	1	1	0
0	0	0	ł	ł	0
0	0	0	1	I	-
0	0	0	1	ł	0
0	0	0	ł	ł	0
0	0	0	ł	ł	4
0	0	0	1		4
0	0	0	0	0	0
0	0	0	0	0	5
Ч	0	Ч	0	Ч	œ
1	1	0	Ч	0	10
Ч	0	0	0	0	16
0	Ч	0	0	1	Ω
0	0	0	0	0	0
0	0	0	0	0	0
0	0	0	0	0	0
0	e	0	0	0	51
0	0		ł	1	4
0	0	ł	ł	1	12
6/22	6/22	6/22	5/21	5/21	
4/13	4/13	4/16	4/16	4/16	otal
25	26	28	29	31	Ţ

^aTrap #'s 1, 6, 8, 10, 11, 12, 14, 15, 17, 18, 21, 27, 30, 32 never took a single CLB; # 10 and 18 non-functional.

Habitat	CLB	Samples	CLB/@	Acres	Total CLB (1,000's)				
Cropland									
Idle ^a	1	3							
Grain stubble ^b	1	3							
Corn stubble ^C	2	1							
Other	0	0							
Subtotal	4	7	2,766	1,303	3,604				
Non-cropland									
Woods edge ^d	70	4							
Fence rows ^e	39	12	32,972	90	2,967				
Roadsides	0	0							
Weeds ^f	4	7	0.744	25	(00)				
Other habitat	0	0	2,766	200	622				
Subtotal	113	23		315 ^g	3,589				
— Total	117	30		1,618 ^g	7,193				
^a Traps #'s:	11,	12, 16.							
^b Traps #'s :	17,	27, 28.							
C									

TABLE 12.--1971 spring adult emergence by habitat at Gull Lake

Traps #'s: 11, 12, 16. ^bTraps #'s: 17, 27, 28. ^cTraps #'s: 5. ^dTraps #'s: 3, 4, 7, 13. ^eTraps #'s: 19, 26, 29, 32. ^fTraps #'s: 1, 2, 6, 8, 9, 14, 15. ^gExcludes 212 acres that is uninhabitable to the CLB.

.

were taken in 16 yd²; 90 acres of this would contain 2,967,000 beetles. Combining these two gives 7,193,000 beetles in the region--an estimate that compares favorably with the results of the extensive population survey reported in Table 16.

Rate of emergence from overwintering

The emergence trap data from Table 11 was summarized into Table 13 to show how emergence from overwintering sites varied with time. Over 50% of the beetles emerged between April 12 and April 21; then an extended cold spell kept any more from emerging until after May 1. Emergence was 92% complete by May 18, but a few continued to show up through June 6.

Plotting the cumulative catch versus date gives an irregular curve (Figure 5a), which suggests that prediction of spring adult emergence is not feasible; however, plotting versus degree-days accumulated above the base of 48° F gives a much smoother curve (Figure 5b). On a log-probability plot (Figure 6) the relationship of cumulative emergence to cumulative degree days is quite linear, if we omit from the analysis the 8% emerging after May 18. This shows that 50% of the beetles should be out by 100 degree days, which in 1971 at Gull Lake was about April 23. Emergence rate (number emerging per degree-day) can be computed from the slope of the linear version of Figure 6, and the resulting curve is shown in Figure 7. Peak emergence occurs in the range from 50 to 150 degree days; if the temperatures were high in this time range, then emergence per day would also be high, but low daily temperatures can result in a low daily emergence even in this peak range because of the consequent low accumulation of degree-days.

		Daily	catch			
Date		Male	Female	Cumulative catch	Accumulated degree days	
April	16	6	6	12	59	
	18	3	1	16	72	
	21	27	24	67	96	
	23	0	0	67	102	
	27	0	0	67	104	
	30	0	0	67	106	
May	5	3	2	72	118	
	7	8	8	88	132	
	10	6	4	98	161	
	15	2	6	106	203	
	18	2	0	108	261	
	22	0	0	108	296	
	25	2	2	112	336	
	29	0	4	116	363	
June	1	0	0	116	403	
	5	0	0	116	491	
	8 ^a	1	0	117	555	

TABLE 13.--1971 spring adult emergence by date at Gull Lake

^aTraps checked through June 22, but no more beetles were found.



Figure 5. Cumulative Emergence from Overwintering Sites at Gull Lake for 1971: a) Over Calander Date, and b) Over Degree-days Accumulated Above the Base of 48° F.



Figure 6. Log-Probability Plot of the 1971 Gull Lake Cumulative Emergence from Overwintering Sites.



Figure 7. Rate of Emergence from Overwintering Sites at Gull Lake for 1971, as Computed from the Observed Cumulative Emergence.

Cage studies of adult mortality

Adult mortality rates measured by the 1970 cage studies (Table 14) were first computed as % mortality over the entire sample interval (M), which varied from 6 to 8 days. Conversion to % mortality per day (M_d) as a standard base for each interval requires the following mathematical equation:

$$M_{d} = 1 - (1 - M)^{1/n}$$

where n is the number of days in the sample interval.

The observed mortality rate began at 7.1% per day, decreased to 3.5% per day two weeks later, then increased again until mid-June; by then the field population was so reduced that it was impossible to collect enough beetles to restock the cages. For newly emerged summer adults the mortality rate began at 10% per day and decreased to 7.4% per day two weeks later. By then the summer feeding period had finished and the beetles were moving into estivation sites.

Next the same data were used to calculate % mortality per degreeday. Degree-days has proved to be a useful time scale in much population dynamics work; in this case it seemed reasonable that survival might be related to temperature, especially if the cause of death is physiological. Table 14 also includes these figures and shows that during most of the spring and summer adult beetle mortality is about 0.4% per degree day.

Regional population survey

The number of cereal leaf beetles estimated to be in the 4 square mile sampling area is reported in Tables 15 and 16 for 1970 and 1971 respectively. Some conclusions can be drawn directly from these tables, but adult mortality is dealt with later in the discussion section.

Date						Mortality (%)		
Fro	m	То	Days	dd ₄₈	Replicate	Total	Per day	Per dd ₄₈
May	7	May 15	8	116	Wl	38.8		
					W2	49.6	/.1	.50
May	15	May 22	7	100	Wl	20.2	5.0	.36
					W2	39.3		
May 22	22	May 29	7	95	Wl	16.8	3.5	.26
					W2	27.1		
May	29	June 4	6	99	01	23.5	6.4	.40
					02	41.2		
June	4	June 11	7	148	01	35.5	8.4	.41
					02	54.6		
June	30	July 7	7	190	01	41.7		
					02	60.7	10.0	4.2
					C1	57.8	10.9	• 4 2
					C2	58.8		
July	7	July 14	7	173	01	37.7		
					02	67.2	0.2	4.2
					C1	36.8	9.2	• 4 2
					C2	57.3		
July	· 14	July 21	21 7	151	01	22.6		
					02	54.7	7 /	26
			C1 53.7		/.4	• 30		
					C2	28.9		

TABLE 14.--Adults mortality as computed from the 1970 cage study

Date	Life stage	Winter ^a grain	Spring ^a grain	Total ^a
June 3	Adult	338	3,466	3,804
June 9	Larva	47,294		
June 23	Larva		15,023	
July	Pupa	23,988	27,804	51,792
July	Adults emerged	7,634	11,007	18,641
June 25	Adult	4,717		
July 2	Adult	4,218	3,860	8,078
July 9	Adult	3,429	8,622	12,051
July 16	Adult		1,186	
July 23	Adult	257	1,040	1,297
Aug. 6	Adult	102	99	201

TABLE 15.--Number of cereal leaf beetles in grain fields in the 4 square mile study area for 1970

^aIn 1,000's.

Winter ^a grain	Spring ^a grain	Total ^a
1,571	N.S.	
1,091	N.S.	
716	6,380	7,096
620	5,601	6,221
873	5,416	6,289
339	2,873	3,212
64	814	878
96	1,108	1,204
66	96	162
17	146	163
80	184	264
9	61	70
12	26	38
42	502	544
101	780	881
380	1,360	1,740
404	940	1,344
263	856	1,119
0	459	459
2	422	424
	Winter ^a grain 1,571 1,091 716 620 873 339 64 96 66 17 80 9 12 42 101 380 9 12 42 101 380 404 263 0 2	Winter grainSpring grain1,571N.S.1,091N.S.1,091N.S.7166,3806205,6018735,4163392,87364814961,108669617146801849611226425021017803801,36040494026385604592422

TABLE 16.--Number of adult cereal leaf beetles in grain fields in the 4 square mile study area for 1971

^aIn 1,000's; N.S. = not sampled.

Sweeping for summer adults in 1970 indicated an estimated peak of 12 million beetles in grain fields. This represents about 65% of the number known to have emerged from the pupae. In 1971 the estimated peak was 1.7 million indicating a 7 fold drop in the population of summer adults from the 1970 level.

Pupal survival in 1970 was lower in wheat (32%) than in oats (40%); however, at high densities the survival is the same in both crops (32%), while at low densities the survival in oats is much better (60%). Figure 8 shows the curvilinear nature of the density dependent survival in oats compared to the constant survival in wheat.



Figure 8. Pupal Survival in Oats and in Wheat at Gull Lake for 1970.

DISCUSSION

Overwintering sites

The adult cereal leaf beetle has been reported to overwinter in a large variety of sites, but attempts to quantify this phenomenon consistently failed to account for the majority of the population. Results presented in this paper show that the surface litter and top 3 inches of soil accounted for no more than 10% of the population, and that those overwintering above ground level in cracks in wood and under wild grape bark sustain an overwinter mortality of about 95%.

If one accepts these data, only two reasonable alternatives exist: either the beetles overwintered outside my 4 square mile study area, or they were in the soil deeper than 3 inches. I think the first alternative is unlikely, partly because the 4 mi² study area contained quite a diversity of habitats, and there is no apparent reason why the beetle would look for an overwintering site elsewhere. The second alternative was never seriously considered during this research because the cereal leaf beetle is obviously not morphologically equipped to burrow in the soil, so it was assumed to overwinter at or above ground level.

During the analysis of the data on overwintering sites, however, I discovered a reference in the literature to a chrysomelid that does overwinter deep in the soil. The Colorado Potato Beetle, which looks even less like a burrower, is known to overwinter as deep as 4 feet in sandy soil (Mail and Salt, 1933) with 10 inches being the average
reported by Harcourt (1963) for his work in Ontario. Furthermore, the beetles don't necessarily have to dig their own burrows; earthworms and nightcrawlers are continually building beetle expressways deep into the soil.

A second reason supporting the hypothesis that the beetles overwinter in the soil can be found in Table 12, the results of the 1971 emergence trap study. Those results indicate that an estimated 7.2 million beetles overwintered in the 4 square mile study area, compared with an estimated 7.1 million present in grain fields on May 19 and 20 (Table 5). This indicates that roughly the proper number of beetles overwintered in the region to produce the observed spring population, and hence suggests that beetles overwintered deep in the soil in the type of habitats sampled using the emergence cages.

So the beetle appears to overwinter deep in the soil, especially in dense fence rows and the edges of woodlots. This is where the beetle density is the greatest. But they also overwinter in cropland such as corn and grain stubble; their density there is low, yet the acreage of that habitat far exceeds that of fence rows and woodlot edges, so the total number overwintering in croplands roughly equals the number overwintering elsewhere.

Adult mortality from survey data

The results of the 1971 population survey for spring adults can be used to compute adult mortality rates. Two assumptions were made as follows: 1) the number of beetles not in grain fields was small enough that it could be safely assumed negligible, and 2) migration into and out of the 4 square mile study area balanced out. Hence any change observed in adult numbers was due simply to mortality.

Computation of mortality would be straight forward except for the fact that 11 of the 22 oat fields were sprayed with insecticide in early June. So the next assumptions made were that all beetles in a field at the time of spraying were killed by the insecticide and that between field adult migration is small, so only the beetles in the field at the time of spraying are affected by the insecticide. The 9 fields sprayed between May 29 and June 2 contained an estimated 1,156,000 beetles on May 29; the 2 fields sprayed between June 5 and June 9 contained an estimated 234,000 beetles on June 5. Figure 9 shows the population curve from May 19 to June 22 after averaging the results for each week. Survival (S) from time t to time t + 1 was computed from

$$S = \frac{N_{t+1} + (1/2)K}{N_{t} - (1/2)K} \times 100\%$$

where N_i is the number of adults present at time i and K is the number killed by pesticide between time t and time t+1. This equation adjusts survival close to what it would have been, if no pesticide had been used in the region. Table 17 presents the results of applying the above equation to the data in Figure 9; % mortality per day and % mortality per degree-day (base 48° F) are also given.

Several differences occur between the 1970 and 1971 adult mortality rates. First, in 1970 there is a time early in the season (see Table 14) when mortality decreases as time progresses. This does not happen in 1971, but this is not surprising because in 1970 sampling began two full weeks earlier in the spring, and adult mortality is expected to be somewhat higher the first few days out of overwintering sites.



Figure 9. Estimated Spring Adult Population in the 4 Square Mile Study Area for 1971.

Date					Mortality (%)	%)
From	То	Days	dd ₄₈	Total	Per day	Per dd ₄₈
May 20	May 27	7	61	28.7	4.7	.55
May 27	June 3	7	93	61.1	12.6	1.01
June 3	June 11	8	163	66.1	12.7	.66
June 11	June 19	8	208	72.4	14.9	.62

TABLE 17.--Spring adult mortality as computed from the 1971 regional population survey

A second difference is that the 1971 observed mortality is consistantly higher than in 1970. Although this may be a real difference, another possibility is that the cages increased longevity by reducing temperatures and/or by exluding predators. Or the 1971 mortality rate may have been overestimated if between field movement of spring adults is greater than expected. Since the two techniques for measuring mortality were not used in the same season, we cannot know if the difference is real or due to technique.

Adult migration from wheat to oats

The cereal leaf beetle is reported to move from overwintering sites to grasses and winter grains and later to spring grains. The question arises whether this movement results from the beetle being attracted to the oats or repelled from the wheat. Also we would like to predict when this movement will occur in any given year.

In 1970 beetles were found only in winter grains prior to about May 10; from May 10 to 18, 20% were in oats; from May 19 to 31, 60% were in oats; and from June 1 to 12, 90% were in oats. This suggests that movement into spring grains does occur, but it is certainly not a rapid process. Observations on the rate of egg input into wheat and oats indicate that oviposition in wheat dropped rapidly to near zero about May 28 while the same occurred in oats about June 15.

In 1971 the proportion of beetles in oats compared to winter grains remained at 90% from May 18 through June 22. Movement into oats occurred gradually from about May 1 to 18, apparently directly from grasses and overwintering sites without going first to winter grains.

On May 29 an estimated 310,000 beetles were in wheat, and by June 2 only an estimated 53,000 remained; that is, 83% had left and/or died in only 4 days. If plant height is an important factor in determining when the beetles leave, then one would expect beetle density to be negatively correlated to plant height on May 29th. The 16 wheat fields sampled on that date gave a correlation coefficient of +.46, which was not significant at the 5% level, so we conclude that the height of the wheat plants has no affect on when the beetles leave.

The 1971 data (Tables 13 and 16) actually suggest that the spring adults do not move from wheat to oats as has been assumed. Emergence from overwintering sites was 50% complete by April 21 and 80% complete by May 10. On May 10 just over 1,000,000 beetles were estimated to be in winter grains; spring grains were not completely sampled because in many fields the plants had not yet come up. In the several oats fields checked, beetle density was relatively low--certainly lower than in wheat. On May 19 and 20 over 7 million beetles were estimated to be in small grains, about 90% of those being in oats, and the population in winter grains had not dropped appreciably since May 10.

So it now seems clear that when the beetles first emerge from overwintering, some portion of the population infests winter grains. The remainder stays in wild grasses or flies around in search of oats until the oats germinate and come up. Then that remainder infests oats. The portion in winter grains remains there, with the observed reduction in density primarily due to mortality not emigration.

The portion of the population that infests winter grains is not constant from year to year. It probably also varies between geographic regions. The primary factor affecting the portion entering winter grains seems to be the size of the plant as it comes through the winter. In 1970 the wheat was very short, and 40% of the beetles went into it; in 1971 it was tall and vigorous, and only 10% of the beetles went into it.

CONCLUSIONS

The simulation model proved to be sufficiently accurate and realistic for further analysis. Several specific conditions that were tested are mentioned below.

The portion of the population preferring wheat affects the generation index (I), because those preferring oats have no available host for oviposition early in the spring, hence their fecundity is reduced. Consequently I is greatest when most or all of the beetles prefer wheat. Available acreages of spring and winter grains also affect I, because of the interaction with the portion preferring wheat and because of its effect on density dependent mortalities; I is greatest when the grain acreages are such that egg input in wheat and in oats is equal.

Temperature has several important effects on the beetle. Exceptionally hot or cold days result in very irregular total incidence curves for the immature stages. More important are the effects on <u>when</u> the population develops and on the generation index. For example, peak larval density in Kentucky is expected to occur a full month earlier than in northern Michigan, and I in Kentucky is expected to be only half of what it is in northern Michigan.

Indirect evidence from field observations suggests that about 80% of the cereal leaf beetle population overwinters more than 3 inches deep in the soil. About half of the beetles overwinter in concentrations along dense fence rows and the edge of woodlots, while the other

half is rather uniformly spread over open areas such as grain stubble, alfalfa fields, and idle grassy or weedy areas. Those beetles that find an overwintering site more than a few inches above ground level, such as under grape bark, are almost totally killed by the low winter temperatures.

Movement of the beetles within the Gull Lake research area progressed as follows: spring adults emerged from overwintering sites over a period of several days, with peak emergence occurring between 50 and 150 degree-days accumulated after April 1 above the base 48° F. A certain portion (10% to 40%) of the population went immediately into winter grains; the rest apparently moved around the environment until the spring grains came up, then infested them. Most or all of the portion that went into winter grains apparently remained there, and the observed reduction in density was due to mortality only.

When the summer adults left the grain fields in July, they soon became inactive and could be found in such protected sites as in leaf litter and grass crowns. As the summer progressed fewer beetles could be found in these sites; apparently most moved into overwintering sites at least three inches deep in the soil.

The spring adult mortality rate is quite small early in the spring and increases as the spring and summer progress. In this paper adult mortality is considered to be determined by the mean daily temperature and the age of the beetle: in early spring 0.2% per degreeday die, while after May 18 the rate is 0.4% per degree-day, and for summer adults the rate is 0.05% per degree-day. Further studies are needed to verify or improve on this estimate of mortality rate.

LITERATURE CITED

LITERATURE CITED

- Bailey, N. T. J. 1964. The Elements of Stochastic Processes with Applications to the Natural Sciences. Wiley, N.Y.
- Castro, T. R. 1964. Natural history of the cereal leaf beetle, <u>Oulema</u> <u>melanopa</u> (L.), and its behavior under controlled environmental conditions. Ph.D. thesis. Mich. State Univ. 121 p.
- Castro, T. R., R. F. Ruppel, and M. S. Gomulinski. 1965. Natural history of the cereal leaf beetle in Michigan. Quart. Bull. Mich. State Univ. Agr. Exp. Sta. 47:623-653.
- Caswell, H. 1971. A classified bibliography of matrix theoretic population models. In Design and Management of Environmental Systems. Unpublished report, Mich. State Univ. 11 p.
- Dickler, E. 1968. The influence of temperature on the survival and development of cereal leaf beetle (<u>Oulema melanopus</u> (L.)) eggs and adults. Unpublished Cereal Leaf Beetle Project Report. Mich. State Univ.
- Dominick, C. B. 1939. Notes on the tobacco Flea Beetle, <u>Epitrix</u> parvula (F.). J. Econ. Entomol. 32:495-498.
- Dominick, C. B. and G. Wene. 1941. Notes on the hibernation of the Tobacco Flea Beetle and on the parasite, <u>Microctonus</u> epitricis (Vier.). J. Econ. Entomol. 34(3):395-396.
- Dominick, C. B. 1971. Overwintering and spring emergence of the Tobacco Flea Beetle. J. Econ. Entomol. 64(1):88-89.
- Gause, G. F. 1934. The Struggle for Existance. Williams and Wilkins, Baltimore. 163 p.
- Harcourt, D. G. 1963. Population dynamics of <u>Leptinotarsa decimlineata</u> (Say) in eastern Ontario: I. Spatial pattern and transformation of field counts. Can. Entomol. 95:813-820.
- Helgesen, R. G. and D. L. Haynes (in press). Population dynamics of the cereal leaf beetle, <u>Oulema melanopus</u> (L.): a model for age specific mortality. Can. Entomol.

- Helgesen, R. G. 1969. The within-generation population dynamics of the cereal leaf beetle, <u>Oulema melanopus</u> (L.). Ph.D. thesis. Michigan State University. 96 p.
- Lefkovitch, L. P. 1965. The study of population growth in organisms groups by stages. Biometrics. 21:1-18.
- Leigh, E. J. 1968. Review of K. E. F. Watt's "Ecology & Resource Management". Science. 160:1326-1327.
- Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika. 33:183-212.
- Leslie, P. H. 1948. Some further notes on the use of matrices in population dynamics. Biometrika. 35:213-245.
- Lotka, A. J. 1925. Elements of Physical Biology. Williams & Wilkins, Baltimore; reprinted 1956 by Dover Publications, N.Y. 460 p.
- Mail, G. A. and R. W. Salt. 1933. Temperature as a possible limiting factor in the northern spread of the Colorado potato beetle. J. Econ. Entomol. 26:1068-1075.
- Miller, C. D. F., S. Gage, and D. Haynes. (in press.) Cereal leaf beetle studies in Canada. 1. Within-generation mortality in artificially established populations. Proc. Entomol. Soc. Ont.
- Odum, E. P. 1959. Fundamentals of Ecology. Ed. 2. Saunders, Philadelphia. 546 p.
- Pielou, E. C. 1969. An Introduction to Mathematical Ecology. Wiley Interscience, N.Y. 286 p.
- Ruesink, W. G. and D. L. Haynes. (in preparation.) Sweepnet sampling for the cereal leaf beetle, Oulema melanopus (L.). Can. Entomol.
- Shade, R. E., H. L. Hansen, and M. C. Wilson. 1970. A partial life table for the cereal leaf beetle, <u>Oulema melanopus</u> (L.), in northern Indiana. Ann. Entomol. Soc. Amer. 63(1):52-59.
- Smith, F. E. 1963. Population dynamics in <u>Daphnia</u> <u>magna</u>. Ecology 44:651-663.
- U.S. Dept. Agric. 1969. Forest insects population dynamics. Forest Service Res. Paper NE-125.
- Watt, K. E. F. 1961a. Mathematical models for use in insect pest control. Can. Entomol. Suppl. 19:1-62.
- Watt, K. E. F. 1961b. Use of a computer to evaluate alternative insecticidal programs. Science. 133:706-707.

- Watt, K. D. F. 1963. Dynamic programming, "Look-ahead programming", and the strategy of insect pest control. Can. Entomol. 95: 525-536.
- Watt, K. E. F. 1964. The use of mathematics and computers to determine optimal strategy and tactics for a given insect pest control problem. Can. Entomol. 96:202-220.
- Watt, K. E. F. 1968. Ecology and Resource Management, McGraw Hill, N.Y.
- Watt, K. E. F. 1970. The systems point of view in pest management. In Concepts of Pest Management. N.C. State Univ., Raleigh. 242 p.
- Yates, F. 1953. Sampling methods for census and surveys. Ed. 2. Griffin, London. 401 p.
- Yun, Y. M. 1967. Effects of some physical and biological factors on the reproduction, development, survival, and behavior of the cereal leaf beetle, <u>Oulema melanopus</u> (L.) under laboratory conditions. Ph.D. thesis. Michigan State University. 153 pp.

APPENDIX

	PROGRAM CLB (OUTPUT, TAPE61=OUTPUT)
	COMMON/SUB/R(10#)
	DIMENSION/E(187),000(187),X0(167) DIMENSION/V0//187),W0//1873,X0//1873,X0//1873,X0//1873,X0//1873
5	DIMENSION AVL(107);XWM(107);XWH(107);XUL(107);XUH(107);XUH(107); CAMHAN/21/WDL(127);WDH(187);WDH(187);ADL(187);ADH(187);ADH(187);
	1 FINL(157), EIWM(187), EIWH(167), EIQL(187), =10H(187), EIQH(187)
	COMMON/R2/D23,D45,D56,D78
	DATA(R(I), 1=1,21)/ -4.0,-1,645,-1,282,-1,036,-0,842,-0,674,-0,524
	1,-0,385,-6,253,-0,126,0,0,0,126,0,253,0,335,0,524,0,674,0,842
10	1,1,036,1,282,1.645,4,0/
	C THIS PROGRAM SIMULATES THE LIFE CYCLE OF THE CEREAL LEAF DEPTLE
15	DO 10 J=1,187
	DDD(I)=0
	$10 \times n(1) = 0$
	C INTITAL VALUES TO BE SET # # # C CLEN # NO CLE ADMITS THAT SUBVIVE THE WINTED
20	
	C DAA = ACRES DF DATS
	C PATIO = PORTION OF BEETLES THAT CHOOSE WHEAT OVER DATS
	<u>C</u>
	CLBN=1000100.
25	WHA=100.
	C DENSITY INDERENDENT MORTALITIES • • •
	C D23 = EGG HORTALITY
30	C D34W= 1ST INSTAR MORTALITY IN WHEAT
	C D45 = 2ND INSTAR MORTALITY
	C 056 = 3R ⁿ INSTAR MORTALITY
	C DO + GVECHINTERING MORTALITY
35	D23=.10
	D34W=.35
	D45=,30
	D56=.40
	D78=,30
40	09 FUDU C THE CHEROLITINGS STANDATE DATEM DENSITIES IN
	C 3 WHEAT AND 3 DAT FIELDS
	CALL HTEMP(TE)
	CALL DEG DAY (DDD, TE)
45	CALL SPR AD (CLPN, WHA, OAA, RATIO, TE, DDD, EWL, EWH, EWH, EOL, EOM, EOH)
	CALL MORT(EWL,EWM,EWH,EOL,EOM,EOH,D340L,D340H,D340H,D67WL,D67WH,
	106/WH,05/0L,06/0H)
	CALL INNA (DRAADORESTESAOSEINGSARES)
50	CALL INMA (D344,D67WH.TE,X0,EIWH.XWH)
	CALL IMMA (D340L, D670L, TE, XO, EIOL, XOL)
	CALL [MMA (D3400,D670M,TE,X0,EIOM,X0M)
	CALL IMMA (D3404,0670H,TE,X0,910H,X0H)
r #	TEI=0.
22	
	D; 20
	1)+X0H(1))/4.+X0H(1)/2.)
	20 TAE = TAE + XO(1)
60	TEI=WHA+43540,*((EWL+EWH)/4,+EWM/2,)+OAA*43560.+((EOL+EOH)/4,+
	1 EOM/2.)
	CALL SUM AU (XU,XWIN,UUU)
	C LIST DAILY RESULTS FOR SPRING ADULT DE'STYLES
55	C AND SUMMER ADULT EMERGENCE.
	WPITE(61,301)
	Do 30 l=1,187

	WRITE (61,302) 1,WDL(I),WDM(I),NDH(I),ODL(I),ODH(I),ODH(I),XWL(I);
70	1XWM(I),XWH(I),XOL(I),XOH(I),XOH(I),TE(I),UDD(I)
	30 CONTINUE
	C
	C COMPUTE AND PRINT YEAR END RESULTS
	C
75	CLBNY=(1,-D9)+XWIN
	AID=CLGN/(WHA+OAA)/43560.
	DS=1XHIN/TAE
	WRITE(61,303) CLBN, CLBNY
	WRITE(61,306) WHA, 044
80	WPITE(61,304) RATIO
•••	WRITE (61.3)7) TEL TAE XWIN
	WPITE(61.303) AID
	WOITE(61,309) B23, D45, D56, D78, D5, D9
	WEITE (A1.310) D344 D34W.D34W.D3401.D340M.D340H.D67WL.D67WM.D67WH
85	10670L 0670H 0670H FWL FWY FWH FOL FCM FOH
0,2	
	U TAA FADDATTANG TAY EDAY BY DAY DESULTES DAY ADAYAA IS ADDIL ACTELAAD
	SUI FORMANIANIANA DA DI DA RESULTA ZON FORMANA AND T PRODUNCTA AND T
90	125X, JSPATEG AUGLI DENSITY, 30X, SUMMER ADOLI EMERGENCEY # 12X,
	134(14+),2%,**8(14+)/* DAT=2(6%,#WL*,8%,*WH*,8%,#WH*,3%,#UL*,8%,*UH*,
	1,8X,#OH#,2X),* TEMP 00#7
	302 FORMAT (14,12F16,6,F5,0,F6,1)
	303 FORMAT (191,30%, YEAR END SUMMARY+/+OSTARIED WITH+, F15, 0, +SPRING A
95	1DULTS +/6X,+AND GOT+,F15,G,+SPRING ADULTS FOR NEXT
	<u>1YEAR+)</u>
	304 FORMAT(+-PORTION OF THE BEETLES PREFERRING WHEAT+,F6,2)
•	306 FORMAT(++4VAILABLE ACREAGE THIS YEAR WAS =+,F10.0,+ OF WHEAT; AND+
	1/34X,F10,00+ CF_0AIS,+)
100	307 FORMAT(+-TUTAL EGG INPUT WAS+, F18,0,+ EGGS,+/+ TOTAL ADULT EMERGEN
	1CF WAS+,F12.0,+ SUMMER ADULTS,*/* *,22X,*AND+,F12.0;* ADULTS WENT
	1 INTO OVERWINTERING+)
	308 FORMAT(+-AVERAGE INITIAL DENSITY ++.F10.44+ PER SQUARE FOOT)
	309 FORMAT(+-DENSITY INDEPENDENT MORTALITIES -+/16X.+EGGS+.F7.2/10X.
105	1+1 2++F9.2/1: Y++1 3++F9.2/10X++PUPAF++F6.2/10X++SUM_AD++F5.2/10X+
	310 FORMATCH-DENSITY DEPENDENT RATES ++.10X.+#HEAT+.41X.+0ATS+//
	27X.* 0W+.5X.+MED1UM+.5X.+MIG
	1H+.17X.+10H+.5X.+MEPIUK+.5X.+HIGH+/12X.+11 MOPI.+.3F10.2.10X.3F10.
110	12/12/14 +14 HORT - 3 - 10 - 2 - 10 X - 3 - 11 - 2 - 11 X - + EGG INPUT + 3 - 10 X - 3 -
+*0	
	E3D
	SUBPOUTINE STADIA (RI,RO,XN,RD,STOR,MORT)
	DIMENSION STOR(100)
	REAL MORT
	C THIS ROUTINE UPDATES THE DEUSITY OF ALL IMMATURE STARES
5	C
	CALL LAG (RT, POUT, STUR, RD)
	RO = FOUT + (1 - RORT)
	XN = XN + RT + CUT
	END
	SUBROUTINE RINEY IR'SIG DWA
	C THIS IS A CASE OF THIS TO A CASE A
	GALANA A FOROTTY ROULINE USED TO GENERATE AN AUTOCOPRELATED
	C SEMPERCE OF NUMBERS,
E	
77	R=R+RH+S10+TASLIE(0,0,0,05,20,2)
	END

	SUBROUTINE IMMA (D34,D67,TE,XOUT,EI,X)
	$\frac{DIMENSION}{S2(100), S3(100), S4(100), S5(100), S4(100), S7(100)}$
	COMMON/R2/D23,D45,D54,D54
5	C ZERO OUT NECESSARY MEMORY:
	R12=0,
	R23≡0.
	R34=0,
	R45E0.
10	R50E0.
15	
	\$2(1)≠0.
	$S_3(1) = 0$.
	S4(1)=0,
	S5(1)=0,
20	<u>\$6(1)*0</u>
	S7(I)=0.
	20 CONTINUE
······	
26	G COMPUTE EPICTIONAL DEVELOPMENT DER DAV FOD FACH LIFE STARP
27	DD(2)=.65+TE(T)=31.6
	PD(3)=1.66+tF(1)=78.8
	RD(4)=RD(3)
	RD(5) = RD(3)
30	RD(6)=RD(3)
•	RD(7)=,26+TE(I)+13,4
	C UPDATE DENSITIES IN EACH LIFE STAGE
	C
	X(I)=R78
35	
	CALL STADIA (R67,K/8,XN(/),RD(/),S/,D/8)
	GALL STADIA (ROGINO/JNIG)JNG/JD0JJ0
40	CALL STADIA (ROS, REALYN(3), RD(3), S3, D34)
10	CALL STADIA (R12, R23, XN(2), RD(2), S2, D23)
	100 812=E1(1)
	END
	SUBPOUTINE SUM AD (RI,XWIN,DDD)
	DIMENSION STOR(100), DDU(187), RI(187)
F	TO STORETIAN.
	C THIS ROUTINE FOLLOWS THE REFUES FROM PUPAL EMERGENCE INTO OVERWINTER
	C ING AND APPLIES A MORTALITY WHICH MUST BE SET IN POP XSURVA . 1
	RD=7.
	XW1N=0.
10	Do 20 I=1,187
-	XSUPV=,9995++NDD(I)
	CALL LAG(RI(1), RO, STOR; RD)
	DO 15 J=1,160
	15 STOP(J)=STOP(J)=XSURV
15	20 XWIN=XWIN+RO
	RETURN

	SUBROUTINE MTEMP (T) Dimension T(187)
5	C THIS ROUTINE GENERATES A MEAN DAILY TEMPERATURE USING AN C AUTOCORRELATED DEVIATION FROM THE LONG TERM AVERAGE
	C J=1 CORRESPONDS TO APRIL 1
10	SIGR=5, RH=0.50 SIG=SQRT(1.0_RH\$RH)+SIGR
	DO 10 J=1,187 CALL RANEX(R,SIG,RH) T(J)=48.+25.+SIN(.0161+FLOAT(J+14))+R
15	10 CONTINUE END
	SUBROUTINE DEGDAY (DD.TEMP) DIMENSION DD(187),TEMP(187)
5	C THE DEGREE DAYS ACCUMULATED,DDD(I),ON DAY I IS COMPUTED FROM THE MEAN C Daily Temperature, Temp(I), by assuming the daily high is 10 degrees C above the mean and by fitting a sine curve thru the max and ming
	CC BASE=48, DO 10 I=1.187
10	DIF=TEMP(I)-BASE IF(DIF.GE.10.) GO TO 20
•	THETA=ASIN(-DIF/10.) DD(1)=3.18+COS(THETA)+DIF+(,5-THETA/3,14)
15	GO TO 10 20 DD(I)=DIF 10 CONTINUE END
	SUBROUTINE LAG IRIN' ROUT. PIPE. RDEV)
	DIMENSION PIFE(100)
5	C THIS ROUTINE COMPUTES A PURE OR PIPELINE TYPE LAG
	C RDEV.IS PERCENT DEVELOPMENT PER DAY ON THIS DATE C Routeb.
10	INC=RDEV+.499 IF(INC.LE.0) GO TO 20 DO 5 I=1,INC
	5 ROUT=ROUT+PIPE() INCM=100-INC D0 10 I=1.INCM
15	10 PIPE(I)=PIPE(I+INC) RINA=RIN/FLOAT(INC) INCP=INCM+1
20	DO 15 1=INCP,100 15 PIPE(I)=RINA RETURN
, A.Y	20 PIPE(100)=PIPE(100)+RIN END

	SUBROUTINE SPR AD (CLBN, WHA, OAA; RATIO, TE, DDD, EWL, EWH, EWH, EOU, EOM,
	1EOH) COMMON/R1/WFL(187),WDM(187),WDH(187),ODL(187),CDH(187),CDH(187))
	1 FIWL(187), FIWM(187), EIWH(187), EIOL(187), EIOM(187), EIOH(187)
5	DIMENSION TE(187), DDD(187)
	C THIS DONTING MONITODS SEDING ADM T DENSITY AND NOVERENT DETHESN SPORT
	C IT ALSO COMPUTES DATLY EGG INPUT INTO EACH OF THE 6 FIFLDS.
10	EWL=0,
	EWM=0,
	EwH=0.
	EOL=0.
15	
* >	DO 10 I=1.167
	WnL(1)=0,
	WDM(I)=0,
	WDH(1)=0.
20	<u>OnL(I)=0</u> ,
	UDM(1)=0, ODH(1)=0.
	FTWL (1)=0.
	EIWM(I)=0.
25	EIWH(I)=0.
	EIOL(I)=0.
	E10M(I)=0,
30.	
•••	C SPRING ADULTS EMERGE FROM OVERWINTERING AT 100 DD BASE 48
	CC
	C IST IS THE DAY OVIPOSITION BEGINS, 10 DAYS AFTER ADULTS FIRST SWOW;
35	C BETWEEN FIELD VARIATION IS APPROXIMATED BY 3 DENSITY CLASSES
	C SEE TEXT FOR DETAILS.
	IF(DD.GF.100.) GO TO 11
	Dn=DD+DDD(1)
40	IF(DD.LT.100.) GO TO 20
	<u>IST=I+10</u>
	WDA=RATIU+CLEN/WHA/43560,
	WOL(1)#.04#WDA UDM(1)=0.4WD(1)
45	WDH(1)=9.**UN(1)
12	07A=(1,-RATIO)+CLBN/0AA/43560.
	C ON DAY 48 THE DATS BECOME AVAILABLE AND THE BEETLES MOVE IN:
	11 IF(1.4E.48) GO TO 12
~ •	ODL(I)=,04*ODA
20	00m(1)=9,*00m(1)
	12 (L.NE.58) 60 TO 13
	12 [F(I.NE.58) GO TO 13 Obl(I)=0DU(I)+0CL(I)+0HAZOAA
	12 IF(I.NE.58) GO TO 13 <u>ODL(I)=ODL(I)+HCL(I)+HA/OAA</u> ODM(I)=OD ¹ (I)+HDN(I)+HA/OAA
55	12 IF(I.NE.58) GO TO 13 <u>ODL(I)=ODL(I)+HOL(I)+HA/OAA</u> ODM(I)=ODH(I)+HDH(I)+HA/OAA ODH(I)=ODH(I)+HDH(I)+HA/OAA
55	12 IF(I,NE,58) GO TO 13 ODL(I)=ODL(I)+#GL(I)+#HA/OAA ODH(I)=ODH(I)+#DH(I)+#HA/OAA ODH(I)=ODH(I)+#DH(I)+#HA/OAA WDL(I)=0, WDH(I)=0
55	12 IF(I.NE.58) GO TO 13 ODL(I)=ODL(I)+HGL(I)+HA/OAA ODM(I)=ODH(I)+HDN(I)+HA/OAA ONH(I)=ODH(I)+HDH(I)+HA/OAA HDL(I)=0, HDM(I)=0, HDM(I)=0.
55	12 IF(I,NE,58) GO TO 13 ODL(I)=ODL(I)+HOL(I)+HA/OAA ODM(I)=ODF(I)+HDN(I)+HA/OAA ODH(I)=ODF(I)+HDH(I)+HA/OAA WDL(I)=0, WDH(I)=0, WDH(I)=0, ON DAY 76 THE BEETLES IN OATS LEAVES
55 60	12 IF(I.NE.58) GO TO 13 ODL(I)=ODL(I)+#GL(I)+#HA/OAA ODH(I)=ODF(I)+#DN(I)+#HA/OAA ODH(I)=OUH(I)+#DH(I)+#HA/OAA WDL(I)=G, WDH(I)=G, WDH(I)=C, C ON DAY 76 THE BEETLES IN OATS LEAVE; 13 IF(I.NE.76) GO TO 14
55 60	12 IF(I.NE.58) GO TO 13 ODL(I)=ODL(I)+#OL(I)+#HA/OAA ODH(I)=ODF(I)+#DN(I)+#HA/OAA ODH(I)=ODF(I)+#DH(I)+#HA/OAA WDL(I)=0, WDH(I)=0, WDH(I)=0, C ON DAY 76 THE BEETLES IN OATS LEAVE; 13 IF(I.NE.76) GO TO 14 ODL(I)=0,
55 60	12 IF(I.NE.58) GO TO 13 ODL(I)=ODL(I)+WOL(I)+WHA/OAA ODH(I)=ODH(I)+WDH(I)+WHA/OAA WDL(I)=0, WDH(I)=0, WDH(I)=0, WDH(I)=0, C ON DAY 76 THE BEETLES IN OATS LEAVE; 13 IF(I.NE.76) GO TO 14 ODL(I)=0, ODM(I)=0,
55 60	12 IF(I.NE.58) GO TO 13 ODL(I)=ODL(I)+HOL(I)+HA/OAA ODM(I)=ODH(I)+HON(I)+HA/OAA ODH(I)=ODH(I)+HON(I)+HA/OAA WDL(I)=0, WDM(I)=0, WDM(I)=0, C ON DAY 76 THE BEETLES IN OATS LEAVE; 13 IF(I.NE.76) GO TO 14 ODL(I)=0, ODM(I)=0, ODM(I)=0,
55 <u>60</u>	12 IF(I.NE.58) GO TO 13 ODL(I)=ODL(I)+HGL(I)+HA/OAA ODH(I)=ODP(I)+HDN(I)+HA/OAA ODH(I)=ODH(I)+HDH(I)+HA/OAA WDL(I)=0, WDH(I)=0, C ON DAY 76 THE BEETLES IN OATS LEAVE; 13 IF(I.NE.76) GO TO 14 ODL(I)=0, ODH(I)=0,
55 <u>60</u> 65	12 IF(I.NE.58) GO TO 13 ODL(I)=ODL(I)+HGL(I)+HA/OAA ODH(I)=ODP(I)+HDH(I)+HA/OAA ODH(I)=ODH(I)+HDH(I)+HA/OAA WDL(I)=0, WDH(I)=0, C ON DAY 76 THE BEETLES IN OATS LEAVE; 13 IF(I.NE.76) GO TO 14 ODL(I)=0, ODH(I)=0, ODH(I)=0, ODH(I)=0, ODH(I)=0, C ON DISCONTO 15 C C ON DUTE ECC INPUT

• •

.

		EIWL(I)=WDL(I)+RT
70		EIWM(I)=WDM(I)*RT
		E1WH(I)=WDH(I)*RT
		ETOL(I)=OPL(I)*RT
		E10M(I)=ODM(I)*RT
		E10H(1)=0DH(1)*RT
75	<u> </u>	COMPUTE SURVIVAL RATE FROM THE PER DD HATE, AND UPDATE ADULT DENSITIES
	1	5 RT=.996++DDD(1)
		IF(I_LE.48) RT=(RT+1.)/2.
		WPL(1+1)=WDL(1)+R1
80		
95	C	UNRELED SUB ALLAN CONTRACT TO STAD THE YEARYS TOTAL FOR LADIT DED SOULDS FOR
65		THIS IS NEEDED TO CONDITE LADAR DATA THE DIRES.
	L L	THIS IS DEEDED TO COMPUTE LARVAL MURIAWITY RATES
		Ex10-Ex10-Ex10-2 ()
91		
,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,		
	2	
	2	
95	-	END
		SUBPOUTINE MORT(EWL,EWM,EWH,EOL,EOM,EOH,D340L,D340M,D340H,D67WL) 1D67MM,D67KH,D670L,D670M,D670H)
	C	THE DUILT CONDUCT THE DEVELTY DEDENDENT NOTICE IN DITECT
F	C C	THIS ROUTINE COMPUTES THE DENSITY DEPENDENT MORTALITY RATES.
2		DIACH -ANAYIAA ANTRIA OO AGAALOCIACIEGI N
	•	
		$D_3 = (D_1 + A_1 + (D_1 + (D$
		D4701 = AMAX1(n, AMIN1(,99, 28+AL0610(F01)=18))
10		D670M=AMAX1(n.,AMIN1(.99,.29+AL0G1n(EOM)18))
		$D_{670H=AYAX1(0,.,AMIN1(.99,.20+ALCG10(E0H)18))$
		D474L=A'AA)(0,,AMIN1(,99,,34+ALCG10(EHL)-,31))
		D67WH=AHAX1(0,,AMIN1(,99,,34+ALOG10(EWH)-,31))
		D67HH=AMAX1(0,,AMIN1(,99,,34+ALOG10(EWH)+,31))
15		RETURN
		END
		FUNCTION TAFLIETSMALL, DIFF, K, DUMMY)
		COMMUN/SUM/VAL(100)
	C	THIS IS A FORDER RULLINE USED TO TRANSFORM A UNIFORMLY DISTRIBUTED
-	C	RANDOM VARIABLE INTO UNE THAT IS MURMALLY DISTRIBUTED.
5		UMPEANINI (ATAXI (DUNMY-SMALL)0,0)41 LCAI(K) DIFF2
		1 = 1, U + U U T / U + F
		1+{1+EW+N+1}#N #
10		END

DAY BY DAY RESULTS

DAY=1 IS APRIL 1ST

N44 N. 904 N. 94 N. 94 N. 94 N. 94 N. 96 N a 5 10100 900000 SUNFF ADDILF FRAFF. SUNFF. S -5

 $\begin{array}{c} \mathbf{G}_{\mathbf{A}} = \mathbf{G}_{\mathbf{A}} \mathbf{G}_{\mathbf{A$.000 . 6.10 c in the ċ c, c c ς. ċ. õ 1 1
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0

 1
 4
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
 0
1

 $\begin{array}{l} & \mathbf{N} \in \mathbf{N} \in \mathbf{N} \in \mathbf{N} \in \mathbf{N} \in \mathbf{O} \in \mathbf{O} \cap \mathbf{N} \cap \mathbf{N} \cap \mathbf{O} \in \mathbf{O} \in \mathbf{O} \cap \mathbf{O} \cap \mathbf{N} \cap \mathbf{O} \cap \mathbf{O} \in \mathbf{O} \cap \mathbf{O} \cap$ i 0110 i. ł 3 - 1 1 1 1 ł 1 ÷. ÷ ÷ 000 1 1 1 1 1 i i 1 1 1 . 1 1 000 0.0 i. 1 1

6 46660443678604 3076994050404080 307699409040508004 30769940940908004 30769940940908004	ระอุณ จยอ 			
5 9 9 9 9 9 1 1 1 2 9 9 9 9 9 9 9 9 9 9 9				
	E C F E E E IF E C F E E E C C C E			
	Constants			S HIGH 0,00 87,10
				4601UM 0400 0400 4412
				0 - 00 - 46 - 46
0 0 0 0 0 0 0 0 0 0 0 0 0 0	00000000 0000000 00000000 00000000 00000	ND OVERWINTE		
	0 0 0 0 0 0 0 0 0 0 0 0 0 0	NEXT TEAR OF WHEAT, A OF GATS, A ADULTS, INTO	F 5001	HIGH • 35 • 75
	Портисти и страниции и страни	ADULTS ADULTS ADULTS ADULTS FR 100. 100. 100.100000000	8 0 () 8 0 ()	ИНЕАТ Ven IUM 1.35 0.03 .93
		01.5PRING 61.5PRING 61.5PRING 61.5PRING 61.5PRING 61.5PRING 745.07 56.2707 56.2707 56.2707 56.2707	- 114 ALTTES -	P CONT
		19000 46390 665 THIS Y 8655 THIS Y 8651 ES P	DENT KSITY	ENT RATES
0.00000 0.00000 0.000000 0.000000 0.000000	0 • 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	ED WITH AND GOT APLE ACREJ DM OF THE EGG INPUT EMULT EME	ITY INTER	LTY DEPENDE
00000000000000000000000000000000000000	204 - 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 2 2 2 2	START AVAIL Porti Total	A VERA	nevsi

80

,

.

