

FOREST INSECT POPULATION DYNAMICS

**Proceedings of the Forest
Insect Population Dynamics
Workshop,
West Haven, Connecticut
23-27 January 1967**



U. S. D. A. FOREST SERVICE RESEARCH PAPER NE-125
1969

NORTHEASTERN FOREST EXPERIMENT STATION, UPPER DARBY, PA
FOREST SERVICE, U. S. DEPARTMENT OF AGRICULTURE
RICHARD D. LANE, DIRECTOR

Foreword

THE PURPOSE of the Forest Insect Population Dynamics Workshop was to permit some probing in depth of forest insect population systems and to provide an opportunity for the exchange of ideas and information in this subject. Organized and developed primarily for Forest Service personnel interested or involved in quantitative population studies of forest insects, the Workshop was augmented by outside scientists especially knowledgeable and experienced in pertinent facets of population dynamics. The program was oriented to the researcher, with emphasis on approaches and methods of analysis, but with due consideration of output and applications.

The format was simple. One day was given to each of four major subject areas. The primary presentations, which comprise the text of this publication (with the exceptions noted below), were given in the mornings, followed by questions, answers, and discussion of the subject.

The presentation of Dr. Wyatt W. Anderson (then with Yale University) on the fundamentals of population genetics and its interplay with population ecology is not included in this Proceedings because of the basic nature of the information and its availability in standard texts. The paper by Dr. Charles L. Remington (Yale University) on the genetic consequences of insect population displacement or transport is omitted also because it has been published in Volume 15 (1968) of the *Annual Review of Entomology*.

Unfortunately the taped recordings of the open discussions could not be transcribed adequately, and so this vital portion of the Workshop cannot be included.

— WILLIAM E. WATERS

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FOREST INSECT POPULATION DYNAMICS— SOME BASIC CONSIDERATIONS

by WILLIAM E. WATERS, Chief, Forest Insect Research
Branch, Forest Service, U. S. Department of Agriculture,
Washington, D. C.

THE STUDY of biological population systems—conscientious and concentrated as it may be—requires a certain philosophical buffering of the sort expressed by this whimsey of Omar Khayam.

Into this Universe, and *Why* not knowing
Nor *Whence*, like Water willy-nilly flowing;
And out of it, as Wind along the Waste,
I know not *Whither*, willy-nilly blowing.

Man probably has always been concerned with changes in the nature and abundance of living things—at least of those things that affect his mode of living and survival. Studies in population dynamics today cover a broad spectrum of taxa, and encompass or merge with many subject matter fields. Most investigations have been—and still are—directed to objects or problem areas that relate to our own welfare: human demography, epidemiology of disease, or the recurrence of pest insects. However, with ample funding, an adequate supply of graduate students and technical assistants, and computer facilities, it is possible at times to investigate population phenomena of little practical consequence but considerable academic or theoretical interest. And, it sometimes seems worthwhile even to probe into the dynamic complexities of purely hypothetical populations.

For good reason, some of the most productive research in population ecology has been conducted in the forest environment. Like the marine environment, which too has been the working ground of some fundamental and meaningful population studies (*Beverton and Holt 1957*), the forest has a continuity in space and time that permits wide-ranging and long-term studies of it as an ecosystem, or of important components within it that may be considered as systems in themselves. Added features are that it

can be traversed thoroughly, and its major constituents can be seen and measured or counted. A corn field or apple orchard has these latter advantages also, but population studies in such environments necessarily are limited in time and place (*LeRoux et al 1963*).

Our field of interest is, of course, forest insects — insects that feed and reproduce in or on forest trees and cause some injury in the process. Most of our major forest insect pests have been looked at quite intensively at one time or another, but very few have been studied continuously for a long enough period to provide adequate data for really meaningful analysis. Detailed, but truncated records have been obtained on the spruce budworm (*Morris 1963*), larch sawfly (*Lejeune 1955*), and gypsy moth (*Campbell 1967*) in this country and Canada, and on a very few forest insects elsewhere, such as the larch budmoth in Switzerland (*Auer 1961, Baltensweiler 1967*)

Now, in developing and carrying out studies of the population dynamics of the gypsy moth in northeastern United States, we have needed to clarify terms and to do a double-take on some of the mathematical models being used or proposed for analytical purposes. And, in moments of real soul-searching we have been compelled to ask just what are we studying here, what are we really after, what is population dynamics anyway?

Let us take a close look at these questions.

Population dynamics, most simply, refers to changes in numbers and, by implication at least, in the qualities of populations of living things.

Then, studies in population dynamics must concern themselves with (1) defining the population in question, (2) measuring the changes in it, and (3) determining the factors causing the changes, or perhaps just associated with them. It is implicit that the population boundaries, the measured changes, and the relations among components be specified, observed, or derived in quantitative terms and that some form of analysis (mathematical or otherwise) be utilized to obtain the desired information.

The most cursory review of the subject will show that the population systems reported on differ in various ways: (1) the

populations range from small and highly discrete, perhaps artificial, segments of a whole population to complete inventories of the whole—the latter is rare, and each case usually is a sample of unknown proportions and representativeness; (2) the objectives of study, as stated for the record, vary in all manner of ways—more often than not they are simply *constraints* or specifications of *limits*, not statements of purpose; (3) the population parameters measured or estimated and the criteria of change are not at all consistent—and they sometimes are not even the proper ones for the stated objective(s); and (4) the methods of analysis, and resultant interpretations, range from oversimplification to incomprehensible complexity.

Within the sphere of forest insects specifically our objectives may be to obtain:

- Insight into the system *per se*.
- Predictors or predictive equations of natural population trends (both short- and long-term).
- Basic information for judging when, where, and how the insect population(s) can be suppressed or regulated by silvicultural practices biotic and chemical control, or other means.
- Some means of predicting long-term outcomes of the foregoing control or regulatory methods—applied singly or in combination—and corollary bases for developing optimal strategy for integrated control programs.
- Other, less well defined purposes.

As to general approach, we may proceed in either of two directions:

Particular → *Whole or General*

This is the traditional approach in forest insect ecology, and in animal ecology in general—exemplified by studies of parasitism and predation, dispersal, fecundity, weather and climate effects, and so forth.

Whole → *Particular*

Biological systems traditionally are viewed as hopelessly complex—except by the population geneticists perhaps—but biologists now are drawing on the optimism and experience in econometrics

and physical systems analysis to attempt this approach—for example, the use of life tables and pertinent multivariate analysis in an orderly sequence (*Morris 1963, Morris 1965, Campbell 1967*).

The objectives cited above may overlap somewhat, so that a study directed to one may provide information relevant to another objective. But it is not possible to be equally successful in regard to *all* objectives. Similarly, whichever approach is taken for whatever objective, model building to maximize realism, generality, and precision may achieve a fair measure of two but not all three of these qualities in any instance. Thus, models of biological populations may be characterized generally as (*Levins 1966*):

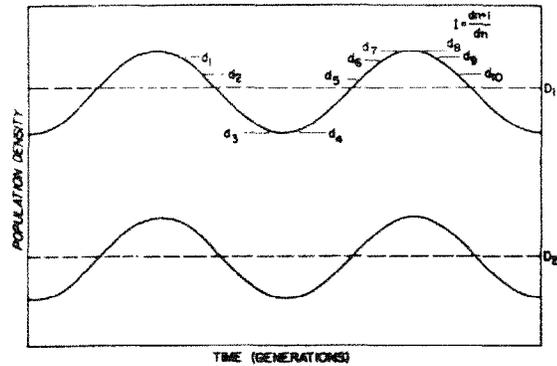
1. High in realism and precision, low in generality.
2. High in generality and precision, not very realistic.
3. High in realism and generality, low in precision.

Strategy in model-building then should be knowledgeable and purposeful, not simply inadvertent, with respect to the particular population system involved and the prime objective of study.

What about the population parameters of interest, the criteria of change, and the bases for evaluating significance or importance of related factors (considered as constants or variables)?

First of all, the data may be in a form unsuitable for analysis. Is a transformation needed—either to fulfill the minimal requirements of a particular analysis (analysis of variance, say) or simply to allow the data to be incorporated into a particular model (for example, transformation to logarithms to convert a multiplicative model into additive form)? Do we need an estimate of the spatial or temporal distribution parameter(s); or are the mean, variance, and derived statistics sufficient? Is sampling error present? Can we estimate it? And if so, how is it entered into the analysis? And what values are to be used for mortality and survival in life tables and in subsequent analyses of them—*apparent* (based on the number of individuals alive at the beginning of an age interval) or *real* (based on the number alive at the beginning of the generation)? To my knowledge, no analyses of life tables of forest insects have been made as yet using *real*

Figure 1.—Schematic representation of oscillations in numbers of two forest insect populations.



mortalities (and survival rates). Different interpretations and/or conclusions as to the "critical" factors might arise from the use of these *real* values as compared with analytical results based on the *apparent* values.

Then, what is the dependent variable? We may be concerned with changes in *absolute (or relative) density* or with changes in *trend in density*. Both are important, of course, in the dynamics of any population system. Both have been given as the dependent variable in recently published theoretical and empirical population models (*Watt 1961, Morris 1963, Campbell 1967*).

Further, in the probing of relationships we find that we may be analyzing the relations of *mean values* (when regression coefficients are taken as the measure of relationship) or the relations of the *variances* of the dependent and independent variables (when r^2 , the coefficient of determination, is used). A difference in concept and interpretation is involved here. When *variability* is the criterion, it becomes axiomatic that any factor having a more or less constant effect over time is not important. And if attention is focused (analytically speaking) on rate of change in numbers rather than density, we may indeed be restricting interpretations. Are we not interested in factors that fix or alter mean density levels, and does it matter whether they act as constants or variables in so doing?

A look at Figure 1 may clarify some of these points.

This is a schematic diagram of changes in density of two forest insect populations, differing obviously in their mean density levels, designated by the two horizontal dashed lines D_1 and D_2 . The points on the upper population curve, marked d_1, d_2, \dots, d_{10} , indicate density at particular times. As indicated, the index of population trend, I , is simply the ratio of two successive densities.

Now, the density level of a particular population may be the same at different times—for example $d_1, d_6,$ and d_9 —and the rate of change too may be about the same at different times in the same cycle or in different cycles—for example,

$$\frac{d_2}{d_1} \text{ and } \frac{d_{10}}{d_9}, \quad \frac{d_4}{d_3} \text{ and } \frac{d_8}{d_7}$$

Moreover, the latter, I values may be identical in two separate populations that differ significantly in mean density level.

The whole population system of any forest insect (or other animal, for that matter) will encompass a spectrum of such point densities and I values, and the models developed thus far to analyze life table data do not distinguish between the values in different subpopulations. All are pooled, and thus relationships may be confounded. Segregation or stratification of life tables by mean density level categories, at least, is needed to resolve this difficulty. More refined stratification should further reduce confounding of time-place effects. Campbell's analysis of gypsy moth life table data has demonstrated the importance of this (*Campbell 1967*).

A more general point can be made from this diagram. Long-term oscillations in population numbers are characterized fully by three basic parameters: (1) mean density level, (2) amplitude, and (3) periodicity. The form(s) of curves for forest insect pests will differ with respect to one or more of these parameters. It is evident that control or regulation can be directed to, or involve, one or all of them. If population regulation is an objective, then we should use all knowledge gained of each insect population system to decide on which pathway to follow—lowering the mean density level, reducing amplitude of the

oscillations, extending the period between peaks of abundance, or any combination of these—and how best to achieve it.

It probably is fitting to close this very incomplete resumé of some basic considerations in the study of forest insect population dynamics with another verse of Omar, the Wise.

Myself when young did eagerly frequent
Doctor and Saint, and heard great argument
About it and about : but evermore
Came out by the same door where in I went.



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APPROACHES TO THE STUDY OF POPULATION DYNAMICS

by R. F. MORRIS, Forest Research Laboratory, Canada
Department of Forestry and Rural Development, Fredericton, New Brunswick, Canada.

THERE ARE MANY approaches to the study of population dynamics. On one scale, they range from the study of a single life system to the study of the whole ecosystem—that is, from the study of a single animal species and only those environmental variables that affect its numbers significantly, to the study of community structure, energetics, or productivity. On another scale, they may be concerned primarily with the proximate causes of year-to-year changes in population density—or primarily with the ultimate, or evolutionary, explanation for the persistence or relative abundance of a species. Most of us whose interest in population dynamics stems from forest entomology tend to work with individual life systems and to develop models based on the proximate variables, and my remarks will be concerned with this aspect of population work.

Several approaches to the development of proximate models for single species have been tested but, in my opinion, no really adequate model has yet been produced. In fact, our work in this field is in such an early stage of development that I don't believe we can even say which approach offers the most promise. One object of our work on forest insects at Fredericton is to test different approaches, and I shall first attempt a brief appraisal of three types of models that have been produced, and then describe some preliminary results obtained from the integrated use of two approaches.

Life-Table Approach

Table 1 presents an example of age-specific models produced by the development of life tables for natural populations (*Morris et al 1963*). Survival (S) is simply population density at the end

Table 1.—Age-interval survival models for the spruce budworm, based on life-table studies

Age-interval survival ¹	Model	Proportion of variation explained
S_E	None	—
S_S	$0.448 - 0.0245 F_d + \frac{1.1123}{N_s} - 0.0533 \log D_{cc}$	0.49
S_L	$[S_{par}] [0.096 + N_L e^{-(4.87 + .009N_L)}] [1.5797 - 0.0396Z]$ $[-3.85 + 6.30 T/H - 1.97 T^2/H^2] [.67 + 0.009 F_i]$.56
S_P	$2.488 - \frac{120.35}{T_{max}}$.60
$2P \varphi$	$0.879 - \frac{28.52}{T_{mP}}$.44
P_F	$100.72 - 0.16 N_L + \frac{89.35}{D_y}$.85
S_A	None	—
S_G	Combined age-interval models	.41

¹ Legend:

- D_{cc} = Cumulative defoliation, obtained by adding values for defoliation of current year's shoots over successive years.
 D_y = Defoliation history of a stand, expressed as the number of successive years in which loss of current foliage was practically 100%.
 F_d = Average diameter of the host trees in a stand.
 F_i = Forest isolation index.
 H = Humidity index for a specified period.
 N_L = Number of large larvae (third instar).
 N_s = Number of small larvae (first instar) per 10 square feet of foliage.
 P_F = The proportion of F that can be achieved by the females of a given population, as revealed by reductions in female size associated with suboptimal feeding conditions during the larval period.
 $P \varphi$ = The proportion of adults that are females.
 S_A = Survival of adults up to and including the time of oviposition.
 S_E = Survival of eggs to eclosion = N_s/N_E .
 S_G = Survival in any generation.
 S_L = Survival of larger larvae (i.e., instars 3, 4, 5, 6) = N_p/N_L .
 S_P = Survival of pupae = N_A/N_p .
 S_{par} = Survival from parasites during a specified age interval.
 S_S = Survival of small larvae (i.e., instars 1, 2) = N_L/N_s .
 T = Temperature index for a specified period of time.
 T_{max} = Maximum daily temperature averaged over a specified period of time.
 T_{mP} = Mean daily temperature averaged over the pupal period.
 Z = Index of phenological development, based on criteria described each time the symbol is used.

Table 2.—"Key-factor" models for the prediction of density in year t+1 from density and other variables measured in year t

Species	Model ¹	Proportion of variation explained
Spruce budworm (<i>Morris et al 1963</i>)	$\log N_{t+1} = 1.37 + .68 \log N_t S_{par} S_{pred} + .14 (T_{max} - 66.2^\circ)$	0.79
Black-headed budworm (<i>Miller 1966</i>)	$\ln N_{t+1} = .714 + .86 \ln N_t S_{par} + .004 (\text{Heat} - 1169^\circ)$.92
European spruce sawfly: (<i>Neilson & Morris 1964</i>)		
Gen 1: Gen 2, same year	$\log N_{t+1} = .65 + .89 \log N_t S_{par} S_{dis} + .12 (R - 6.73'')$.85
Gen 2: Gen 1, next year	$\log N_{t+1} = 1.04 + .64 \log N_t S_{par} S_{dis}$.60

¹ Legend:

N_t = Number of insects in a given stage in any year t.

N_{t+1} = Number of insects in the same stage in year t+1.

S_{par} = Survival from parasites during a specified age interval; i.e., 1—proportion killed by parasites.

S_{pred} = Survival from predators during a specified age interval; i.e., 1—proportion killed by predators.

S_{dis} = Survival from disease during a specified interval; i.e., 1—proportion dying due to disease.

T_{max} = Maximum daily temperature averaged over a specified period of time.

Heat = Degree-days measured as daily mean temperatures less 42° F. accumulated for the period June 1 - August 20.

R = Number of inches of rainfall in any year.

of an age-interval divided by that at the beginning, and the dependent variables in the left-hand column refer to the survival of eggs, small larvae, large larvae, pupae, the sex ratio and fecundity, the survival of adults and, finally, the survival of the whole generation. I don't propose to discuss these models in any detail but only to refresh your memory as to their general form.

Characteristic of this approach is a rather massive, and almost continuous, sampling program designed to provide estimates of population density for as many stages as possible in the life history of the insect. The independent variables are generally selected in two ways. First, historical information on the past behavior of the population, including the pattern of damage, suggests certain hypotheses as to the factors affecting density. Then a fishing expedition is conducted, using the regression techniques on which the model is based, to see whether additional variables can be found that appear to have a significant effect on survival.

"Key-Factor" Approach

Table 2 shows examples of a simpler type of model, based on what I call, for want of a better name, the "key-factor" approach (*Morris 1959, 1963*). Only one population fix is obtained during each generation, based on the developmental stage of the insect that best lends itself to sampling. Then regression methods are used to obtain the best predictive equation for population density in the next generation (N_{t+1}) from population density (N_t) and other key variables in the present generation. Actually, this approach is similar to the life-table approach. The independent variables are selected in the same way and the main point of difference is that, as a result of the reduced frequency of sampling, age-specific sub-models are not possible. Some workers, such as Varley and Gradwell (*1960*) use methods that are intermediate between the two.

"Process" Approach

Table 3 presents some models based on what I call, again for want of a better term, "process" studies. Here the investigator, instead of concerning himself with the whole life system, has

Table 3.—Examples of some different types of "process" models to explain the number of insects attacked by parasites or predators

(1). *Deductive (Nicholson and Bailey)*

$$N_A = N \left(1 - e^{-\frac{a'P}{N}} \right)$$

(2). *Deductive - inductive (Watt)*

$$N_A = PK(1 - e^{-aNP^{1-b}})$$

(3). *Components analysis (Holling)*

(Summary of fragmental equations)

Hunger:

$$H = HK \left(1 - e^{-\frac{AD(TF)}{H}} \right)$$

or

$$H = HK + (HO - HK)e^{-AD(T)}$$

Shape of the reactive field:

$$r_a = r_o / (1 + C\theta^2)$$

Area of reactive field:

$$\begin{aligned} A &= KA(GM(H - HT))^2, & H > HT \\ A &= 0, & H \leq HT \end{aligned}$$

Speed of movement of mantid:

$$VD = 0$$

Speed of movement of prey:

$$VY = (V_{max} - V_{min}) e^{-a_v N_o} + V_{min}$$

Capture success:

$$SC = (SR)(SS) e^{-m(TP)}$$

Time spent pursuing prey:

$$\begin{aligned} TP &= (KR(GM)(H - HT) - DS)/VP, & H > HTP \\ TP &= 0, & H \leq HTP \end{aligned}$$

Time spent eating each prey:

$$TE = KE(WE)$$

CONTINUED

Table 3.—Examples of some different types of "process" models to explain the number of insects attacked by parasites or predators (Continued)

Time spent in a "digestive" pause:

$$TD = \frac{1}{AD} \ln \frac{HK - HO}{HK - HT}, H < HT$$

$$TD = 0, \quad H \geq HT$$

Legend:

For Models (1) and (2)

- N_A = Number of prey attacked.
 N = Initial number of hosts or prey vulnerable to attack.
 P = Number of parasites or predators actually searching.
 K = Maximum number of attacks that can be made per P during the period the N are vulnerable.
 a, a', b = Constants.

For the Fragmental Equations of (3)

- A = Area of reactive field of predator.
 AD = Rate of food disappearance or rate of digestion.
 a = Rate of successful search.
 C = A constant relating to functional operation of compound eye.
 θ = Angle of prey to body axis of predator.
 DS = Strike distance.
 GM = Constant relating distance of perception to hunger.
 H = Hunger, as measured by the weight of food required to satiate the predator.
 HK = Maximum capacity of gut.
 HO = Hunger level after prey is consumed.
 HT = Hunger level at which searching for prey begins.
 HTP = Hunger level at which pursuit begins.
 KA = Areal constant relating area of the predator's field of reaction to the distance of reaction at $\beta = 0^\circ$.
 KE = Feeding rate (time per unit weight of food eaten).
 KR = Equals KA/π .
 m = Constant relating success of pursuit to duration of pursuit.
 N_0 = Prey density.
 r_a = Maximum distance of awareness of prey by predator.
 r_n = Maximum distance of reaction to prey directly in front of predator.
 SC = Success the predator has in capturing prey that enter its perceptual field.
 SR = Recognition success of the success of recognizing a prey that enters the predator's perceptual field.
 SS = Strike success or the success of capturing a prey once a strike is made.
 T = Time.
 TD = Time taken in a digestive pause after a prey is eaten.
 TE = Time spent eating each day.
 TF = Time of food deprivation timed from a condition of complete satiation.
 TP = Time spent in pursuing each prey.

CONTINUED

Table 3.—Examples of some different types of "process" models to explain the number of insects attacked by parasites or predators
(Continued)

V_{\max}	=	Maximum velocity of prey at $N_0 = 0$.
V_{\min}	=	Minimum velocity of prey at $N_0 = \infty$.
VD	=	Average velocity of predator during searching.
VP	=	Average velocity of predator during pursuit.
VY	=	Average velocity of prey during pursuit.
WE	=	Weight of each prey eaten.

concentrated on a population process with the object of explaining the mode of action of a certain mortality factor. Most of the early models, such as the one proposed by Nicholson and Bailey (1935) were purely deductive and do not provide good fits to actual field data. The deductive-inductive model of Watt (1959) was derived with good field data in hand, so that different deductive ideas about the mode of action of parasites could be tested for goodness of fit. This model provides an excellent description of the rate of attack of certain spruce budworm parasites, but goodness of fit, by itself, does not necessarily mean that the model provides a correct explanation of the process. In the very detailed components analysis used by Holling (1966) the process is broken down into its basic components, and theory and experiment are used hand in hand in order to derive a detailed description and explanation of the process.

It is a curious fact that process studies to date have been mainly confined to parasitism, predation, and competition. When we look for similar studies on physical factors affecting insects we find that some very useful work on behavior and development rates has been done, but few attempts have been made to explore the causal pathways through which these factors affect survival rates or population quality.

Appraisal of Approaches

Now I should like to make a brief appraisal of these approaches, with particular regard to the models in tables 1 and 2:

(1) The models are empirical and purely descriptive, not ex-

planatory. To use only one example, the model for the survival of small larvae (S_s) in table 1 contains F_d (average tree diameter) as one of the independent variables. It does so only because F_d explained more of the variation in survival than did the other stand factors that were measured. It was recognized, however, that mean diameter was related to the amount of foliage per acre, the production of staminate flowers on balsam fir, the number of trees per acre, and the exposure and microclimate of individual crowns. If the causal mechanisms through which stand factors affect survival were known, it should be possible to measure the appropriate variables and to refine this preliminary model to one that would have more biological meaning.

- (2) Although sampling error was appreciable, most of the variation in survival not explained by the spruce budworm model could be attributed to failure to measure all the relevant independent variables, or failure to measure them in the best way. This comment, like the first, is related to the methods used for selecting and measuring the independent variables.
- (3) My third comment is also related to the first. Interactions among the independent variables are mainly ignored in the model. Since causal pathways were not adequately understood, it was difficult to make reasonable assumptions about modes of interactions.
- (4) Most models developed to date suggest that one, or perhaps two, age intervals are critical, and that a few key variables operating in these periods account for most of the variation in generation survival or rate of population change. Thus, although there are many advantages in having models for all age intervals when this is possible, models of the key-factor type might be adequate for many purposes if we had better information of the process type.
- (5) The models developed to date for any one species apply to rather limited areas or forest types. Simultaneous population studies over areas where climate and vegetation are very different should lead to models that are more complete, and

also more useful for examining the possibilities of control through environmental manipulation. That is, models should explain population differences associated with place, as well as with time.

- (6) Finally, with a few exceptions, most models suggest that there has been very little liaison between population workers in the field and process workers in the laboratory.

It is very easy to be critical, of course, with the omniscience of hindsight, and it is not my intention to disparage the models that have been presented so far by various workers. They represent a very great advance over the qualitative and purely verbal descriptions of life systems that preceded them. I am only interested in considering ways in which they might now be improved.

Approach to Studies on *Hyphantria cunea*

It seems clear that considerable improvement would be possible if field sampling and experimental process studies were to proceed hand in hand as integral parts of the same investigation. The field work would show the relative importance of different key variables that require detailed study, and provide the final test of the predictive powers of the model; while the process work would establish cause and effect, show the best way to measure the independent variables in the field and to model their effects in the analysis, and probably suggest additional variables that should be measured.

The fall webworm, *Hyphantria cunea* Drury, is a good test animal for an integrated approach of this sort. The nests are large and conspicuous at the peak occurrence of the fifth instar, and in New Brunswick and Nova Scotia, where there is only one generation a year, an annual census can be conducted rapidly over large and diverse areas. This leaves most of the year free for process work. Colonies can be established in different situations and at different densities in the field for detailed observations, or reared in the laboratory where such factors as temperature, humidity, and food quality can be controlled in any combination—including combinations that place considerable stress on the popu-

lation. This permits the development of laboratory life tables showing the immediate effect of any stress on a particular stage, as well as the delayed effects on later stages or on later generations.

Some Effects of Heat on *Hyphantria cunea*

The population density of the webworm at any time or place is determined largely by the joint action of five factors, and of these the effects of heat on survival are the most important and also the most complex. To illustrate the type of information provided by the integrated approach, I am now going to list some of the pathways through which heat affects webworm survival. I am using *heat* as a convenient term for the number of degree-days above the webworm's developmental threshold of 51°F., and you should bear in mind that my objective is to develop and test models that will predict—and explain—changes in the population of nests in any area from year to year (that is, from any year, t , to the next year, $t+1$).

- (1) *The rate at which heat is accumulated in any year, t , has direct effects on survival in t and fecundity in $t+1$.* Heat is accumulated rapidly at high temperatures and slowly at low temperatures, and departures from the webworm's optimum of about 80°F. reduce larval survival, pupal size, and adult fecundity. These relationships, as well as the interaction between heat and humidity, have been derived from life-table studies at both constant and variable temperatures and need not be discussed further at this point.
- (2) *The amount of heat in t has direct effects on survival to the census period in t .* Figure 1 shows the occurrence of adults, fifth-instar larvae, and pupae in the field in relation to heat accumulation in a warm year, and figure 2 shows contrasting values for a very cold year. The webworm overwinters as a diapausing pupa in the ground and the moths emerge in June and July. The nest census is conducted at the peak of the fifth instar. The broken lines, based on known heat requirements, represent mortality due to an insufficient accumulation of heat for development.

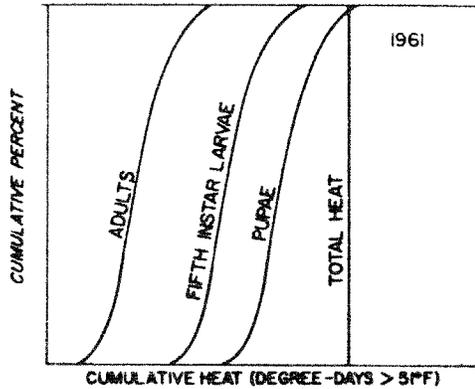


Figure 1.—Occurrence of adults, fifth instar larvae, and pupae of *Hyphantria cunea* in the field in relation to heat accumulation in a warm year.

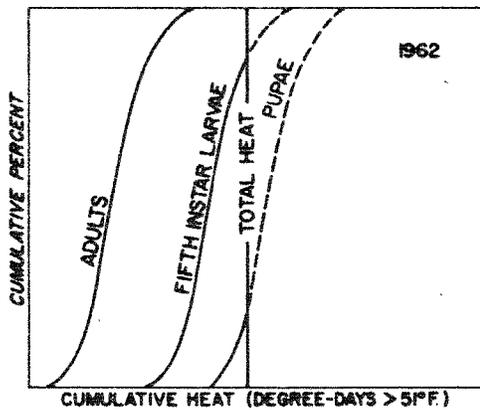


Figure 2.—Occurrence of adults, fifth instar larvae, and pupae of *H. cunea* in the field in relation to heat accumulation in a cold year.

In the cold year, 1962, the progeny of late-emerging adults did not even reach the fifth instar before the end of the developmental season.

- (3) Heat in t has direct effects on survival after the census period in t and hence on the initial population density of $t+1$. Figure 1 shows that even in warm years in the Maritime Provinces a small proportion of the population may fail to reach the overwintering pupal stage. In cold years (fig. 2) this proportion becomes very high.

These last two effects of heat are simple and direct, and can be modeled easily, provided the heat requirements of each stage have been carefully determined for both laboratory and field colonies. Their effects on population density can be seen by looking ahead to figure 5, with attention only to the solid lines representing area A. Observe that nest population declined in the cold year, 1962, because some colonies were unable to produce discernible nests; and again sharply in 1963, because many colonies failed to reach the pupal stages in 1962. Note that the scale is logarithmic; the total reduction in population between 1961

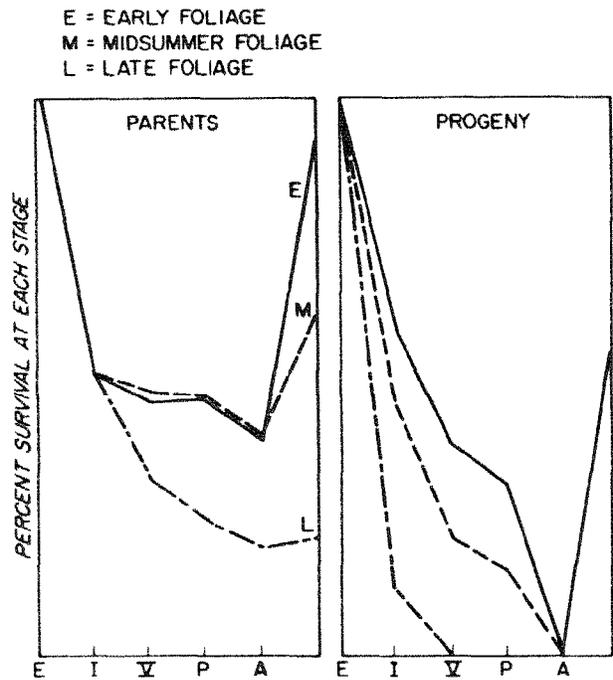


Figure 3.—Survival to successive stages when larvae of the parental generation are reared on early, midsummer, and late foliage collected from the same trees (left side); and survival of progeny of the same three series when the progeny were reared on a deficient synthetic diet (right side). On the bottom scale, E = eggs, I = instar, V = instar, P = pupae, and A = adults.

and 1963 was 99%, largely attributable to lack of heat in 1962.

- (4) *Heat in t has indirect effects on survival in t , operating through food quality.* Figure 3, left side, shows the survival to each stage—eggs, I—instar, V—instar, pupae, and adults—when larvae of the same genetic stock are reared under controlled conditions on early (E), mid-summer (M), and late (L) foliage collected from the same trees. The age of foliage usually available to natural populations in the Maritimes varies between M and L, depending on the accumulation of heat. Thus in cold years when feeding has to extend into the late fall, survival is reduced.
- (5) *Heat in t has indirect effects on fecundity in $t+1$, operating through food quality.* This is also shown in the left side of figure 3, where the F represents percentage of possible fecundity. The females of series E produced 600 eggs each, series M about 60% of this, and series L only 20%.
- (6) *Heat in t has indirect effects on survival in $t+1$, operating through a transmitted maternal influence on population quality.* The right side of figure 3 shows the survival of the progeny of the three series on the left, when the progeny were all reared under identical conditions on a deficient synthetic diet. When the parental generation had early foliage, the progeny survived and produced eggs; when it had midsummer foliage, they failed to produce viable adults; and when it had late foliage, the progeny did not reach the fifth instar. When some of the same progeny were reared on foliage in the field, similar results were obtained. That is, maternal food quality had important effects, especially on the viability of the eggs and the survival of the larvae. Thus, when two equally cold years occur in succession, a realistic model should provide for lower survival in the second year because the resistance of the population to additional nutritional stress has been lowered.
- (7) *Heat in t has indirect effects on survival in $t+1$, operating through the influence of nature selection on heat require-*

ments. To explain this, I wish to introduce the term "eclosion heat," which is simply the mean amount of heat required by webworm pupae each spring before the moths will emerge. Each fall larvae are collected from the different census areas, the resulting pupae are overwintered at 35°F, and the progress of moth eclosion is recorded under controlled temperatures the following spring. When it appeared that the heat required for eclosion varied not only from area to area but also from year to year within an area, I suspected at first that it was an artifact associated with collection or rearing methods. However, records for wild adults taken in light traps showed exactly the same trend of variation. Figure 4 is based on light-trap records for a number of years in one area, and it appears that the heat required for eclosion in the spring is determined partly by the total heat of the previous summer. The assumption that this is a result of natural selection is based on the following points:

- (a) The required eclosion heat is under genetic control. When like moths are mated, the progeny have the same heat requirements as the parents and when unlike moths are mated, the progeny have heat requirements mid-way between those of the parents.

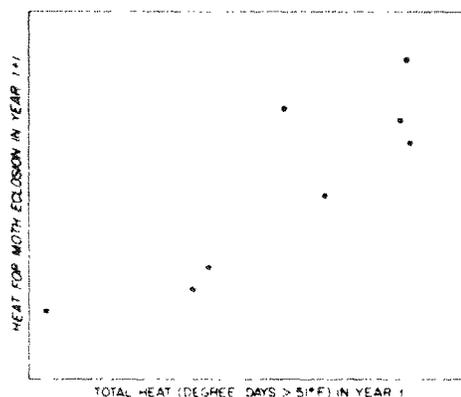


Figure 4.—The relationship of mean eclosion heat required in any year to the total heat accumulation in the preceding year.

- (b) Experimental rearing in environmental chambers is not yet completed, but so far there is no evidence that environmental factors affect the eclosion heat requirements.
 - (c) Figure 2 shows that there is a very high selection pressure in a cold year against the progeny of the adults that emerge late, and hence against individuals that require the most heat for eclosion. Thus, after a cold year, the mean eclosion heat required by the population is considerably reduced as shown in figure 4. Although the rate of change seems very rapid for a selection process, it should be observed that mating is highly assortative rather than random. That is, since the moths live for only about 8 days, the probability is high that early moths mate with early moths, and late with late.
 - (d) In a long, warm season, on the other hand, selection should operate against forms that complete development too early. Dispausing pupae lose weight rather rapidly (about 10% per month at 65°F.) before cold weather sets in, and are also exposed to a longer period of severe predation by small mammals. It should be mentioned, however, that figure 4 is based largely on a population that has gone from a warm period to a cold period. The rate at which heat requirements will increase again is not yet known.
- (8) *Heat in $t-1$, $t-2$, etc. affects population quality in t .* If it is true that there are considerable differences in population quality from year to year and from place to place, arising both from selection and from maternal effects, then presumably quality depends not only on events in the past year but also on events in a number of earlier years. The data have not yet been analyzed to test the significance of such historical effects, but a comparison of the graphs in figure 5 will serve to indicate the possibilities. Area "A" is coastal and has a long developmental season; "B" is inland, the season is always shorter and there are greater deviations

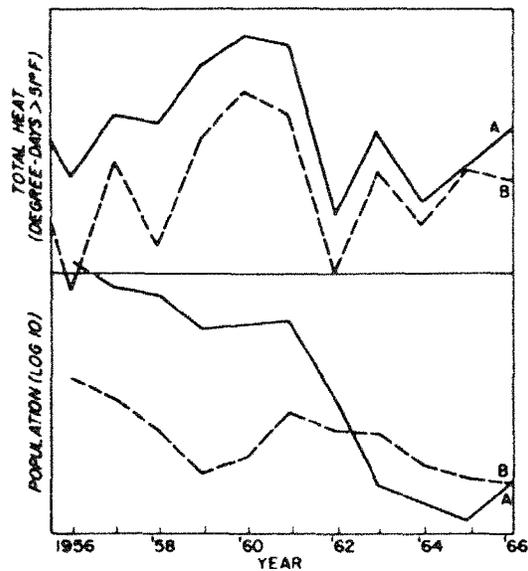


Figure 5.—Total heat accumulation in two study areas, A and B, in the Maritimes from 1956 to 1966 and corresponding population densities in this period.

from the mean, such as those of 1956 and 1958. In both areas, populations increased during the warm years of the early 1950s to a peak in 1956 of about 100 nests per mile in A and 10 nests per mile in B. The cold summer of 1962 was exceptional for A and the population (fig. 5) was reduced by 99%, as described earlier. But population B, which had experienced similar stresses a few years earlier, showed only a moderate reduction. Parasitism and predation in the two areas were not appreciably different during this period. However, heat requirements for eclosion were much higher in A than in B before the population crash, but rather similar afterwards. It is therefore reasonable to suspect that the differential effect of 1962 on the two populations is related to their earlier history. In other words, the longer the population goes without stress, the less prepared it is, qualitatively, when the stress comes along. I have plotted only two areas but similar trends were obtained in five other areas, all leading to the seemingly paradoxical conclusion that the best place to look

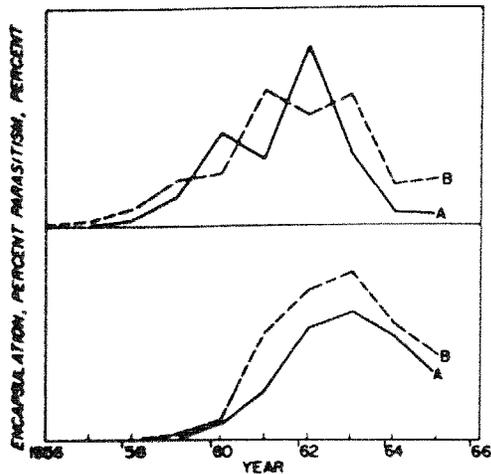


Figure 6. — Percentage parasitism of webworm larvae by *Campoplex validus* in areas A and B from 1956 to 1965 and the percentage encapsulation of *C. validus* eggs over the same period.

for the webworm in times of scarcity, such as 1964-65, is in areas like B where the climate is rigorous, not in favorable areas like A.

- (9) *Does heat affect the degree of parasitism?* Figure 6 shows the percent parasitism of webworm larvae by *Campoplex validus* in Areas A and B, and raises some very interesting questions. Where was *Campoplex* during the high webworm populations of the mid-1950's? And why did *Campoplex* increase simultaneously and give about the same level of parasitism in A and B, as well as in the other five areas in the Maritimes, regardless of differences in host density that ranged from less than 1 to nearly 100 nests per mile? This is not the type of interaction that would be expected from a "classical" parasite, or the type that has been demonstrated for some of the effective parasites attacking the European spruce sawfly or black-headed budworm. *Campoplex* has a considerably lower eclosion threshold than *Hyphantria* and we are testing the possibility that its increase over large areas may be related more to synchronization and weather than to host density.
- (10) *Does heat affect the degree of encapsulation of Campoplex eggs?* The encapsulation of *Campoplex validus* eggs by

webworm larvae was first observed in 1958, increased to 80% in area B in 1963, and then declined (fig. 6). A very limited number of experiments in cages suggests that large host larvae may encapsulate eggs more readily than small ones, and if this is supported by further work it will show one mechanism through which synchronization, and hence the accumulation of heat above contrasting thresholds, determine the abundance and effectiveness of the parasite.

Appraisal of Approach

In conclusion, ten pathways through which heat may influence the population density and quality of *Hyphantria cunea* have been listed, although some of them are still speculative. The other variables affecting this species will not be discussed, because my object has been only to illustrate the sort of relationships that may be disclosed through a very close integration and cross-fertilization between laboratory process studies and field measurements in areas of diverse climate and vegetation.

It is too early to say whether or not the degree of predictability will be improved through this greater knowledge of causal pathways and processes. A graphical analysis of earlier webworm oscillations in this area suggests that simple empirical models would give some degree of predictability, even if based on such a rough index of heat as mean summer temperature, and even without any knowledge of how heat affects survival. And by the same token, some of the empirical key-factor models of table 2 provide surprisingly good predictability.

It is reasonable to expect, however, that predictability will be improved because the process work has shown how and when heat should be measured. For example, it is clear that we are concerned not only with total heat in year t , but also heat in $t+1$ up to the census period. We are concerned with heat in a number of past years because of its two effects on population quality. We are concerned with the seasonal distribution of heat. And we are concerned with the accumulation of heat above different thresholds because of the way that this affects synchronization

between the webworm and its food quality, as well as the webworm and its parasites.

In addition to showing how to measure and express the independent variables, the process studies have also suggested limits and forms of functions by means of which their effects on survival may best be modelled. For example, high maximum temperatures in mid-summer can have adverse effects on the webworm, especially when associated with low humidity. For this reason it has been necessary to develop a computer program that will accumulate heat units between different temperature thresholds. Similarly, some insight into the nature of interactions has also been gained.

And most important of all, if the mathematical task of incorporating the different causal pathways into the final model is not too complex, the model should represent a higher level of biological meaning than could be achieved through regression analyses based on field data alone. My hope is that it will be good enough for reliable simulation studies, with the object of learning whether or not density dependence represents an essential aspect of the webworm's system of regulation and what would happen if sequences of warm years extended beyond their normal expectancy. As a result of the effects of natural selection on heat requirements, webworm populations that are increasing during a series of warm years become progressively less able to take advantage of these favorable conditions. It will be instructive to learn how much the genetic parameters in the model, by themselves, contribute to population stability. Finally, it can be shown that population density is related to land use, vegetation types, and other variables which have not been discussed above. It will, therefore, be worthwhile to employ simulation and minimization techniques to see whether cultural manipulation of the environment can be used feasibly to reduce webworm damage.

Note: The results presented above for *Hyphantria cunea* are based on examples drawn from more extensive data and are intended only to illustrate the approach. The more rigorous mathematical analyses that are planned for the whole body of data may alter the form of these freehand trends.

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STUDIES ON GYPSY MOTH POPULATION DYNAMICS

by ROBERT W. CAMPBELL, Entomologist, Forest Insect
and Disease Laboratory, Northeastern Forest Experiment
Station, Forest Service, U. S. Department of Agriculture,
Hamden, Connecticut.

LIFE TABLES for the gypsy moth were accumulated on 53 generation-years from an area in northeastern New York between 1958 and 1963. Tables 1 and 2 represent typical fates of a cohort from a single egg mass under dense and sparse population conditions.

Table 1.—Life table typical of dense gypsy moth populations in Glenville, N. Y.

x	lx	dx	dx	100qx
Age interval	Number alive at beginning of x	Factor responsible for dx	Number dying during x	dx as percent of lx
Eggs	250	Parasites	50.0	20
		Other	37.5	15
		Total	87.5	35
Instars I-III	162.5	Dispersion, etc.	113.8	70
Instars IV-VI	48.7	Parasites	2.4	5
		Disease	29.2	60
		Other	12.2	25
		Total	43.8	90
Pre-pupae	4.9	Desiccation, etc.	0.5	10
Pupae	4.4	Parasites	1.1	25
		Disease	0.7	15
		Calosoma larvae	0.9	20
		Other	0.4	10
		Total	3.1	70
Adults	1.3	Sex (S:R = 30:70)	0.9	70
Adult ♀♀	0.4	—	—	—
Generation	—	—	249.6	99.84

Table 2.—Life table typical of sparse gypsy moth populations in
Glenville, N. Y.

x	lx	dx _f	dx	100q _x
Age interval	Number alive at beginning of x	Factor responsible for dx	Number dying during x	dx as percent of lx
Eggs	450	Parasites	67.5	15
		Other	67.5	15
		Total	135.0	30
Instars I-III	315	Dispersion, etc.	157.5	50
Instars IV-VI	157.5	Parasites	7.9	5
		Disease	7.9	5
		Other	118.1	75
Total			133.9	85
Pre-pupae	23.6	Desiccation, etc.	0.7	3
Pupae	22.9	Vertebrate predators	4.6	20
		Other	2.3	10
Total			6.9	30
Adults	16.0	Sex (S:R=65:35)	5.6	35
Adult ♀♀	10.4	—	—	—
Generation	—	—	439.6	97.69

These life table data were stratified in two ways: first, on the age interval survival rates of female insects only; and, second, by density class. These stratifications preceded our main analyses.

Inferences about the system were drawn from relationships between variation in density and variation in and among its components. Variance components were partitioned by a procedure proposed by Gordon Mott.¹

Analyses were performed through four levels: first, to identify the age interval survival rates most closely related to changes in population numbers from generation to generation; second, to identify the mortality-causing agents or processes most closely

¹ Mott, D. G. THE ANALYSIS OF DETERMINATION IN POPULATION SYSTEMS. *In* SYSTEMS ANALYSIS IN ECOLOGY. pp. 179-194. New York: Academic Press Inc. 1966.

related to these survival rates; third, to develop models for these agents or processes; and fourth, to use the foregoing in an attempt to describe or analyze long-range trends.

Some specific results from the first analytical level may clarify the above. The variables used in the generation model are shown in table 3, while the components of variance in density of female eggs at the beginning of a second generation are shown separately for dense and sparse populations in table 4.

The results of these analyses can be summarized:

- Variation in the survival rates of the instar IV - VI female larvae and pupae constituted the greatest sources of variation in density among dense populations. Variation in the survival rate of both instar I - III and IV - VI female larvae was most important among sparse populations.
- Disease was the primary determinant of variation in the survival rate of dense populations of instar IV - VI female larvae, while agents other than disease or parasites were most im-

Table 3.—Variables used in the age-interval model of changes in gypsy moth numbers from one generation to the next

$$\log N_{qE(n+1)} = \log N_{qE(n)} + \log S_{qE} + \log S_{qr} + \log S_{qL} \\ + \log S_{qpp'} + \log S_{qp'} + \log F_q$$

where:

$N_{qE(n+1)}$ = Number of female eggs per acre at start of generation (n+1)

$N_{qE(n)}$ = Number of female eggs per acre at start of generation (n)

S_{qE} = survival rate of female eggs

$S_{qr} = (S_{qn} \cdot S_{qpp(pred)} \cdot S_{qp(pred)} \cdot S_{qA})$

S_{qL} = survival rate of large female larvae

$$S_{qpp'} = \frac{S_{qpp}}{S_{qpp(pred)}} = \frac{\text{Survival rate of all female prepupae}}{\text{Survival rate of female prepupae from vertebrate predation}}$$

$$S_{qp'} = \frac{S_{qp}}{S_{qpp(pred)}} = \frac{\text{Survival rate of all female pupae}}{\text{Survival rate of female pupae from vertebrate predation}}$$

F_q = Number of female eggs deposited per adult female

S_{qA} = Survival rate of adult females to commencement of egg deposition.

