DEVELOPMENT OF MANAGEMENT CONCEPTS IN PARASITE SYSTEMS

by

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ABSTRACT

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Biological control is recognized as an essential component of integrated pest management programs. However, for the most part, it is not operational in most agricultural production systems. In this study generalized system designs are formulated for the management of parasites. Concepts are generated concerning the ecology of different classes of parasite-host systems and management of those systems.

Data were collected from a prototype system composed of the eastern tent caterpillar, fall webworm, and a parasite common to both pests, *Campoplex validus*. Analysis of this natural system proceeds with descriptive statements concerning the phenology and survival of the discrete components of the system. Interactions between components are examined using a simulation model capturing development and survival characteristics, as well as, density relationships.

The model is validated using actual field data including: temporal occurrence, larval population maturity, survival patterns, yearly population trends, and trends in parasitism rates. Sensitivity analyses are performed primarily considering the components of parasite-host synchrony and how management of parasites can be effected through alterations in synchrony.

Analysis of the tent caterpillar-webworm system showed that an expanded system conceptualization is necessary for understanding the determinants of parasitism. Thus, the basic one-to-one parasite-host interaction is important, but host-host interactions may ultimately explain the majority of the variability in this multiple host system.

Once the analysis of the tent caterpillar-webworm system was completed, a framework was produced to conceptualize various types of parasite systems and considerations for management of those systems.

The study as a whole emphasizes the need to view each management option (i.e., parasites/predators) as though it were the objective of control. By doing so, there is a need to increase the complexity of system design concepts and consider all factors impinging on parasite production as potentially controllable.

To my parents, Forrest and Wilma
and my wife, Susan

You made it all possible.

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INTRODUCTION

Since its conception, biological control has been looked on theoretically as the most desirable method of controlling pest populations. Classic examples, such as the introduction of the vedalia beetle for control of cottony cushion scale, demonstrated that such methods were viable control options. However, reviews on biological control suggest that these successes are infrequent and for the most part, not operational in agricultural production systems (Beirne 1975, Monroe 1971, Turnbull and Chant 1961). Because of this, pest control methods employing pesticide applications represent the only reliable management option. Presently, this type of energy input into agroecosystems is relatively inexpensive. However, geometric increases in development costs for new compounds, a shrinking energy budget, increased pesticide resistance and concern for environmental quality are generating further interest in non-chemical management techniques and the promotion of an integrated pest management (IPM) philosophy.

The acceptance of IPM dictates an optimal combination of management techniques taking into account constraints occuring internal and external to the system. Keeping this in mind, it is necessary to research each management option as though it were the "object of control" and consider all variables impinging on its efficacy. By doing so, resources are focused on those factors determining the trajectory of parasite populations as opposed to past efforts focusing on pest numbers. Using this approach, parasites and predators become controllable variables and manipulation of numbers and attack rates is possible. This outlook differs from previous concepts in the following way. Using classical methods, parasite introductions are followed only by the assessment of populations in terms of percent parasitism. Therefore, parasites are controlled at the instant of release. Further, in those instances where manipulations are made to control (increase) parasitism (e.g., with food sprays), the state of the system is not sufficiently known and cannot be "fine-tuned" toward desirable population levels.

The inadequacy of our knowledge of parasite systems and the inability or unwillingness to deal with a significant amount of system complexity has given managers little capacity to make predictive statements concerning parasite performance. Assuming that models can be formulated to make predictions for each component of a system, we can look at profit as the objective function and manage the system as a whole in an anticipatory fashion. Without this predictive ability it is clear that we are locked into making short term decisions on long term ecological problems. At best, we will only be able to determine what "has been" rather than what "will be."

In this study parasites will be viewed as the object of control resulting in an explicit appraisal of factors determining parasite numbers and consideration of those factors in the management of parasites. Specifically, the goal of this research is to determine the major management concepts and techniques necessary for successful implementation of biocontrol agents in agroecosystems. This will be accomplished by determining the role that parasites play in population regulation in a real world system. The system selected for study includes the eastern tent caterpillar, the fall webworm and a parasite common to both pests. Analysis will proceed with descriptive statements concerning individual components followed by a simulation model examining population interactions.

Information gained from the analysis will be used in re-evaluating concepts of parasite systems in ecological and management contexts.

THE EASTERN TENT CATERPILLAR-FALL WEBWORM SYSTEM

Problem Statement

Regulation of host populations depends on the host's ability to accept or reject successful parasite attack. Some hosts pass through susceptible life-stages very rapidly and in this way avoid parasitism. Conversely, other organisms move very slowly through time and avoid parasitism through a large variability in temporal occurrence. As a population progresses through different stages of development, mortality factors act differentially on those stages. Thus, age-specific behaviors interact with mortality factors to produce characteristic survivorship curves. Parasites occuring internal to their host experience these same patterns of mortality. If we plan on developing management programs for parasites, it is clear that techniques involving timing and mortality patterns will be of utmost importance. For a monophagous parasite our only concern is the temporal placement of the one-to-one interaction and related mortality patterns. In a multiple host system one-to-one relationships are important, however, indirect effects between host organisms are also of significance (i.e., host-host interactions). This is particularly true in systems where host organisms are separated in time, and multivoltine parasites experience different survival strategies in different generations. In these examples, the number of parasites produced to attack a given host are largely determined by the previous host. Therefore, understanding the dynamics of the system and its ultimate management is dependent on the one-to-one interaction as well as host-host relationships. Keeping the above concepts in mind, objectives for this study fall into categories of system definition, description of development and survival characteristics, and analysis of population interaction. These studies lead to determining a parasite's role in population regulation.

System Definition

The system chosen for study includes the eastern tent caterpillar (ETC) (*Malacosoma americanum* (L.)), ugly nest caterpillar (UNC) (*Archips cerasivoranus* (Fitch)), the fall webworm (FWW) (*Hyphantria cunea* (Drury)), and a complex of multivoltine polyphagous parasites native to the state of Michigan. The parasite pool contains only those species which attack at least 2 hosts throughout the course of a season. Therefore, other parasites, predators, pathogens, etc., become part of the biotic environment which is not explicitly included within this system. Other environmental factors include solar radiation, precipitation, temperature and any other abiotic variables driving the system.

Figure 1 portrays the universe of concern showing the potential parasite-host interactions, gross temporal occurrences, and environmental stimuli.

Within the parasite pool each generation of the individual species is represented by discrete rectangles (Fig. 1). Larger vertical enclosures pertain to the potential parasite guild attacking any one particular host. The term potential is used because the composition of each guild may change as a function of time and geographic location. This listing merely represents documented one-to-one interactions from which we hypothesize

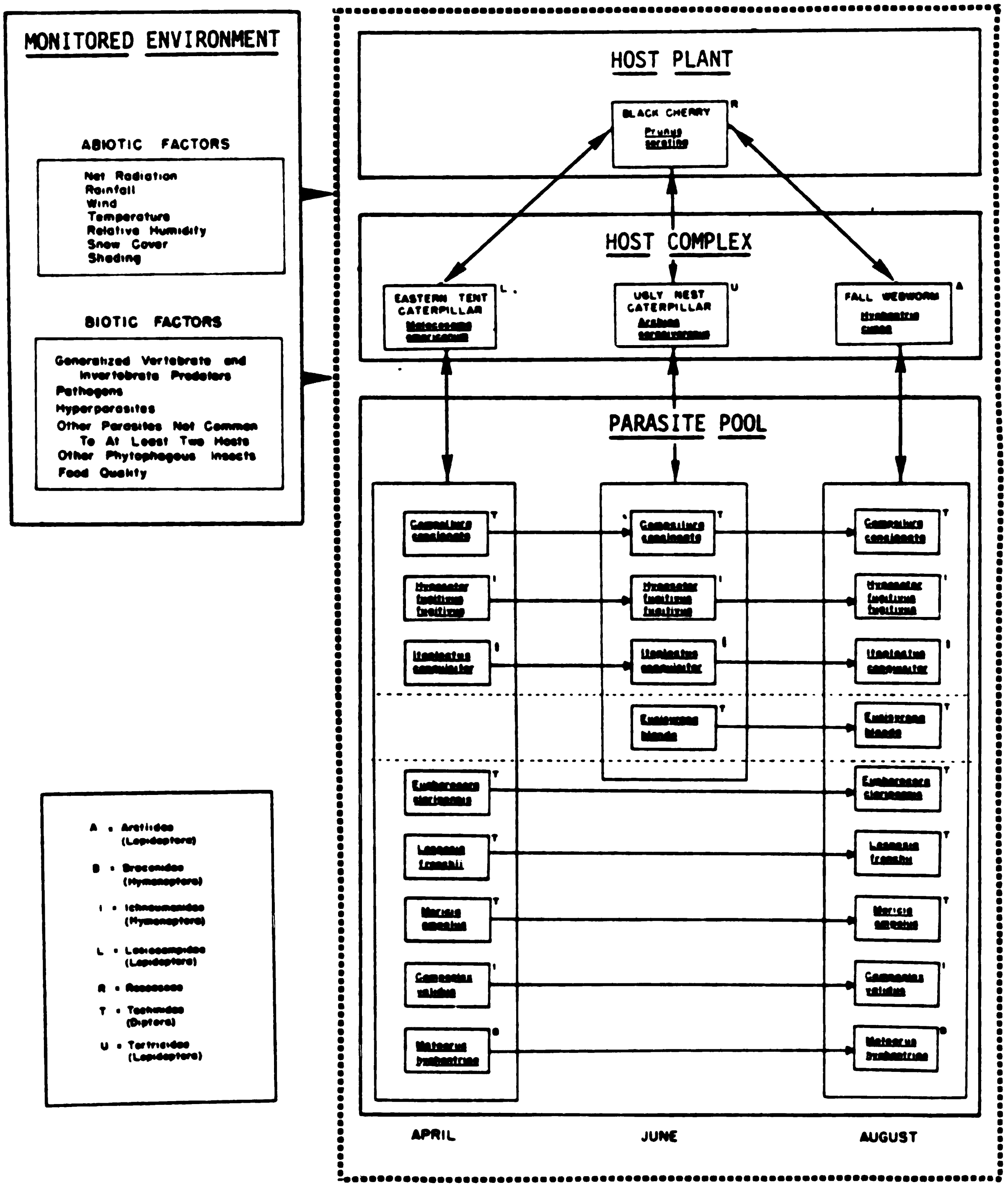

Figure 1. Potential parasite-host interactions, gross temporal occurrences and environmental stimuli.

population flow in the manner described. Information for Figure 1 was taken principally from Muesebeck et al. (1951) and Witter and Kulman (1972).

If each member of the defoliator complex was included along with all parasite species, the basic understanding of the system would be obscured. A sufficient amount of complexity must be retained while eliminating components lacking data and detracting from the objective of determining the parasite's role within the system.

The tent caterpillar and webworm are clearly dominant in the succession of hosts. Baseline information is available from the literature as well as from preliminary data gathered in this study. A parasite common to the ETC and FWW is Campoplex validus (Cresson). C. validus was chosen for study on the basis of its multiple host characteristic along with availability of basic ecological information. Figure 2 presents the gross aspects of the defined system. The plant component, wild black cherry (WBC) (Prunus serotina Ehrh.), is included in this conceptualization and further examined in the subsequent discrete component analysis. However, explicit inclusion into the interaction model is not done due to lack of information on plant-herbivore relationships. Effects of the plant are taken into account in development and survival coefficients and considered as static estimates.

Previous Studies in the ETC-FWW System

Information concerning the dynamics of the ETC is fragmentary. Research has been directed primarily at natural controls including parasites, predators (Witter and Kulman 1972) and pathogens (Clark 1958, Nordin 1974, 1975, 1976). There are no studies which examine population

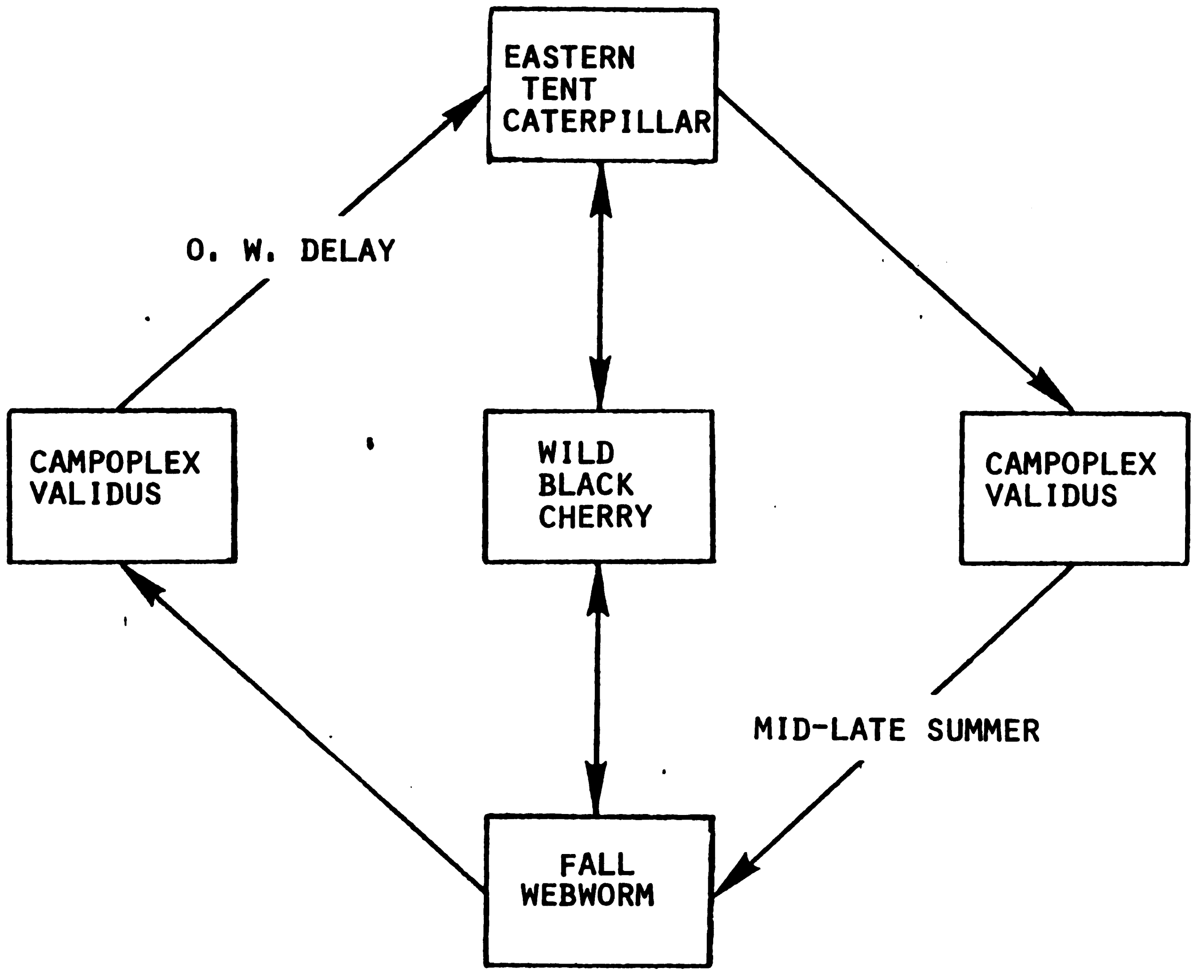

Figure 2. System model depicting the flow of parasites and hosts through time.

processes in this species of *Malacosoma*. Because of this limited treatment, one may only theorize as to the dynamics of the ETC based on research done on a related species, *M. califoricum pluviale* (Dyar), the western tent caterpillar (WTC).

Wellington's (1960) analysis of the WTC indicates that populations are made up of a number of different types of individuals. There is a gradient ranging from larvae which are very active, consume large amounts of foliage, and have a high survival value to sluggish individuals having an overall decrease in fitness. Regional populations may be represented by a frequency distribution of activity which, in part, characterizes the fitness of the population. Changes in the distribution and its magnitude occur as a function of mortality factors such as parasites, predators, and weather variables. Simulation studies point to the retention of desirable character states in portions of the population which are able to avoid these mortality factors. This ability appears to be highly correlated with varying degrees of habitat heterogeneity. Portions of WTC populations which are vigorous enough to seek out spatial refugia are selected for activity and other correlated fitness responses (Wellington et al. 1975, Thompson et al. 1976, 1977, 1979).

The ETC exhibits many of the same traits as the WTC, producing colonies of varying levels of activity, occuring in approximately the same temporal position, and feeding on the same kinds of roseaceous host plants. Furthermore, many of the parasites attacking the WTC in the west are conspecific or congeneric with the eastern species. For example, *Hyposoter fugitivus pacificus* Cushman attacks both the WTC and FWW in the west. Similarly, the ETC and FWW are attacked in the east by a subspecies of *H. fugitivus*, *H. f. fugitivus* (Say) (Langston 1957, Muesebeck et al 1951, Witter and Kuhlman 1972). Even though there are some minor variations in species composition between the two systems, many of the parasite-host interactions that apply to the WTC-FWW system may well apply to the ETC-FWW system.

Much research has been done concerning population processes in the FWW. As early as 1917 Baird reviewed its distribution and natural history. Tothill (1922) examined the parasite complex, and Morris from 1965 through 1976 produced a series of models examining development and survival.

Other significant works on the FWW have been conducted in Japan entitled "Biology of *Hyphantria cunea* Drury in Japan" (Ito and Miyashita 1968). For the most part, these latter works verify Morris' findings and put them in the context of lifetables for the Japanese environment. Other studies conducted in various parts of the world are listed in Warren and Tadić (1970). It should be noted that much data are available for incorporation into a comprehensive model. With this in mind, emphasis is placed on examining the FWW in Michigan as it relates to other parts of North America and particularly its place in the ETC-FWW system.

Methods

Analytical approach. The analytical approach used is that of the "systems approach" (Churchman 1968). This approach is an explicit problem-solving methodology utilizing a succession of model development, validation, and reformulation of those models. There are two prominent attributes of the systems approach: 1) it overtly seeks to include all factors which are important in arriving at a "good" solution to the given problem; and 2) it makes use of quantitative models whenever deemed appropriate. Therefore, in addition to qualitative thinking, it includes computer simulation techniques, mathematical systems theory, stochastic models, and optimization techniques (Varadarajan 1979).

With reference to parasite systems or ecological systems in general, the approach described finds its maximum value in hypothesis generation and data summarization. In addition, if at any point in time we are able to provide probabilistic statements concerning any given performance criterion, we are that much closer to explaining 100% of the variability in nature. This latter aspect should only be viewed as a goal with our objective to pose interesting questions relevant to real world problems.

Plot layout and sampling program. Field studies were performed in and around the Kellogg Biological Station (KBS) located in Kalamazoo and Barry Counties, Michigan. Three major study areas were selected at the KBS. These sites are typical of what might be termed an "old field ecosystem" (Odum 1959). These are areas of land which were once in agricultural production and have since been allowed to revert back to a natural state. The 3 plots at the KBS have been out of production for approximately 30 years and are characterized by varying densities of wild black cherry and to a much lesser extent choke cherry (P. virginiana L.), American crab apple (Malus coronaria L.), and black walnut (Juglans nigra L.). Because these stands have a relatively open canopy, a significant amount of light is able to reach the "forest" floor and hence promote growth of many herbs such as Solidaga spp. Queen Anne's lace (Daucus carota L.), and common ragweed (Ambrosia artemisiifolia L.).

Each of the 3 plots was subdivided into 5 subplots based on characteristics such as tree density, openness and geographic separation. Subdividing the major plots made it possible to examine characteristics of subplots in terms of densities of the eastern tent caterpillar, fall webworm and the parasite complex. In addition, sampling was facilitated allowing random sampling of much smaller areas, as well as providing the ability to partition and reduce variance terms in population parameters (see Appendix E). Positions and areas of each subplot are presented in Appendix D.

The sampling program was developed around a 2 phase scheme. The first phase involved host population density estimates for both the entire larval population and individual colonies. To accomplish this, absolute counts of the number of colonies in each plot were made after the population had established itself. Along with this, weekly samples were taken of 15 whole colonies and the number of larvae recorded. This produced an absolute number of colonies within the study area, estimates of the larval population, and estimation of individuals per colony.

Phase 2 dealt with the determination of parasitism rates. Within each subplot 5 colonies were selected at random. From these colonies, 14 larvae were removed and returned to the laboratory for dissection, totaling 350 larvae per sample period (week). Dissections were done under a stereoscopic microscope, recording the head capsule width of the host, whether or not the larva had been parasitized, and if so, the species of parasite. Data concerning the parasites themselves included visual estimation of instar, the position in the host larva's body cavity and whether or not the parasite had been encapsulated. Along with routine dissections, selected numbers of larvae were reared under laboratory conditions. This provided adult parasites for species determinations along with developmental information on both host and parasite.

Appendix E presents the necessary methods used in deriving estimators for parasite and host population means and variances.

Development and survival. Studies to determine developmental and survival functions were conducted under both field and laboratory conditions. Developmental rate functions were determined in the laboratory and later compared with field derived incidence curves.

Because the egg stage in the ETC is of utmost importance in initializing sample programs, much more extensive rearings were done on this life-stage. Ten egg masses were placed in each of 6 temperatures ranging from 45° F (7.22° C) to 95° F (35.29° C). Each egg mass was monitored daily with the number of individuals emerging recorded. Listing of this rearing data and determination of developmental temperature threshold are presented in Appendix C.

Survival rate functions were determined under field conditions. This was done by obtaining weekly samples of both whole and partial colonies and deriving stage specific incidence curves. The area under each stage specific curve (N_i) was calculated and divided by the developmental time of that particular instar (Eq. 1) (Southwood 1978).

$$N_i = \left[\left(\overset{t}{\Sigma} \frac{N_i(t)+N_i(t-dt)}{2} \right) dt \right] / D_i \qquad [1]$$

The results of these calculations were determined for each instar and compared with the results of the previous instar. Survival rates for each life-stage were calculated by equation 2.

$$S_i = N_i/N_{i-1} \qquad [2]$$

Survival was also calculated in a continuous manner (i.e., as a function of physiological time). This was done by determining the number of individuals per tent for each sample period producing a survivorship curve. Problems and applications of this technique will be reviewed in a later section.

Due to the fact that the FWW was occurring at endemic levels, larval sampling was optimized so as to create only minor changes in colony density without sacrificing information content in the sampling program. In order to achieve this goal, census' began after the population had reached a weighted mean instar (WMI) of 3.5 (see Eq. 13). This allowed reasonable estimates to be made on the early state of population parameters through back-calculations. For example, emergence time of the adult stage can be determined from the knowledge of the instar of an individual and the developmental requirements to that particular life-stage. Since we do not know how long a webworm has been in an instar, we must assume median values for degree-day accumulations along with a normal distribution of counts.

Changes occurring after a WMI of 3.5 were analyzed in a direct manner through weekly samples. These samples were treated as specified by the sampling program previously described.

Measurement of leaf area. Coincident with weekly host and parasite samples, measurements were taken of leaf growth in wild black cherry (WBC). At the beginning of each season 9 WBC trees were selected for monitoring of leaf area. From each of these trees, 1 branch was chosen. All leaves were counted on each branch and length and width measurements of 20 randomly selected leaves were taken. This method of measurement was chosen because initial study indicated it had a high correlation with actual leaf area as measured electronically (Li-Cor®). It allowed rapid accurate estimates to be made without destructively sampling or taking equipment to the field. The relationship between the length times width (L x W) and metered leaf area (A) is shown in Figure 3 with

$$A = (0.8819)(LxW)^{0.9125} \qquad r^2 = 0.9646^*. \tag{3}$$

Basic modeling techniques. The development of lifestages of the insects are highly correlated with the prevailing weather conditions, i.e., temperature, humidity, etc., the predominant factor being temperature. Development takes place only when the temperature ($T(t)$) exceeds a threshold T_0, which is characteristic for that particular insect species. Thus, each life-stage requires a specific amount of heat accumulation (DD) above the threshold T_0, in order to pass from one stage to the next. These heat accumulations are expressed in "degree-days" (D-D). When the temperature profile is given, the degree days are calculated as follows:

$$F(t) = \text{MAX}\ [0,(T(t)-T_0)]\forall T(t) \tag{4}$$

Specifically, the mean delay in days, DEL to move from one distinct life-stage to another, is dependent on the heat accumulation in degree-days, TDD. That is,

$$TDD = \int_0^x F(t)dt \tag{5}$$

where "x" represents the mean number of calendar days required to complete development in a lifestage.

If it is assumed that the growth rate is linearly related to the temperature above the threshold, then the instantaneous value of the

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*For clarity many equations have been returned to the original units of measure. Coefficients of determination (r^2) throughout this discussion apply only to transformed equations.

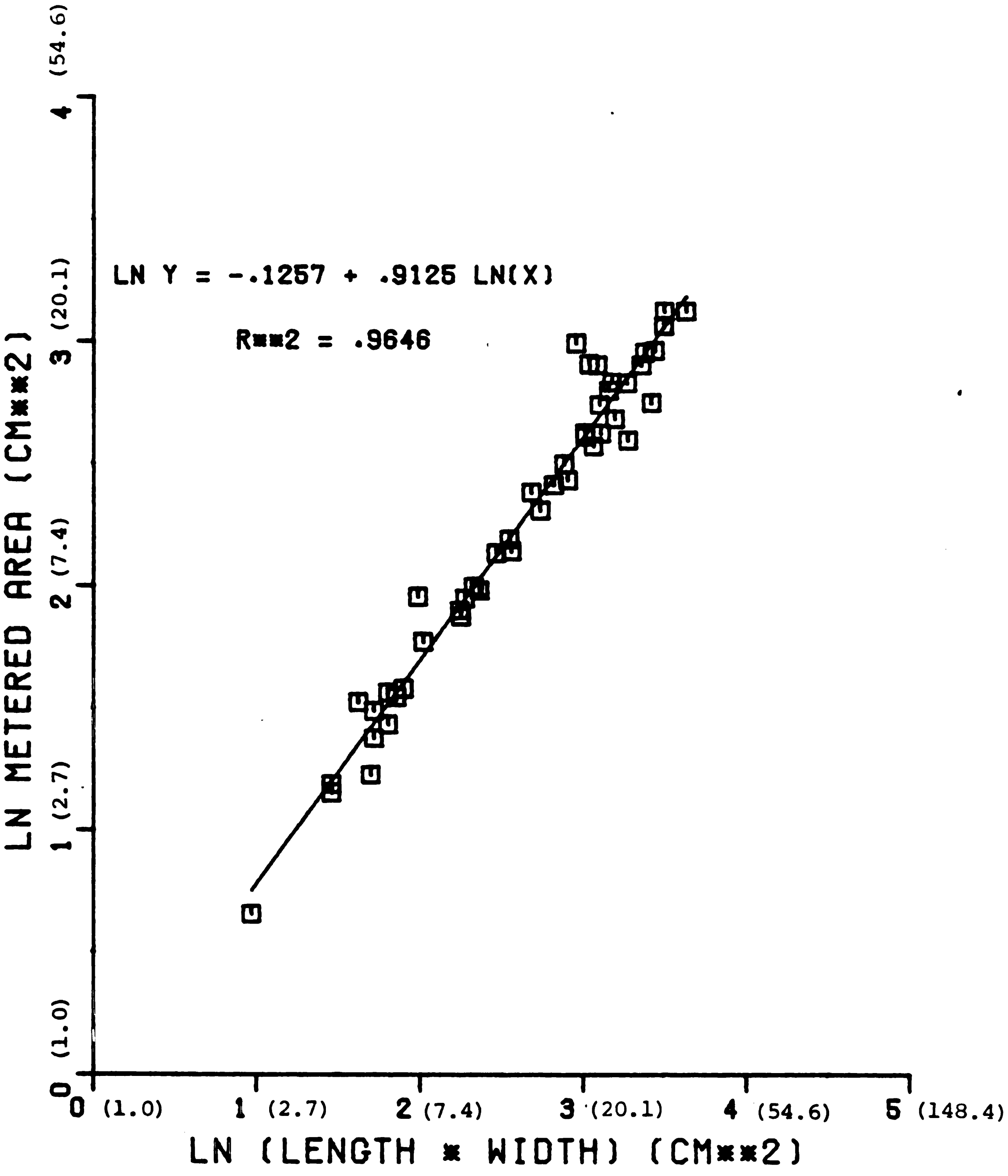

Figure 3. Relationship between length times width and actual leaf area in WBC.

maturation delay (the inverse of the rate of growth), DEL(t), is given by:

$$DEL(t) = TDD/MAX[0,(T(t)-T_0)] = TDD/F(t). \qquad [6]$$

However, it is not necessary to make the above assumption, or to restrict ourselves to considering temperature alone. Developmental velocity curves that provide information on the maturation rates for insects with reference to weather parameters, can be used in conjunction with "table look-up functions," to obtain instantaneous values of DEL(t), for given weather parameters (Fulton 1975). Otherwise equation 6 can be used. The threshold temperature (T_0), the heat requirement in degree-days (TDD), and developmental velocity curves are easily estimated from laboratory and field studies. Once the developmental rates are estimated, the development of the insects in general can be modeled as discrete delays using difference equations or delay-differential equations. The underlying assumption in using a discrete delay to model insect development is that <u>all</u> individual entities of the insect population at any one stage develop in an identical manner. In other words, it is assumed that the insects move as homogeneous groups from one life-stage to another. In reality, this is seldom the case. Insects develop as heterogeneous groups, and hence there exists differences in development between individuals. Therefore, it is more realistic to model the developmental delays of insects by modeling their aggregative behavior which is characterized by a mean delay and associated variance. For insects this mean delay is dependent on temperature and is time-varying. Consequently, the basic building-blocks of the subsequent simulation model are time-varying distributed delays (Forrester 1961, Abkin and Manetsch 1972, Manetsch 1976). In general, distributed delays are useful in modeling processes that are: 1) irreversible, and 2) described by flow-rates or aggregates of entities that move at different rates through a given process.

The two important parameters that completely specify a distributed delay are DEL and k. DEL is the expected value of the transit time of an individual entity through a process. In other words, DEL is the mean of the probability density function describing the transit times of the population of entities. The parameter k specifies a member of the "Erlang" family of density functions that is used to describe the transit times. The Erlang density function is given by:

$$f(\tau) = \frac{DEL^k}{k} (\tau)^{(k-1)} \exp\left(- \frac{k\tau}{DEL}\right) / (k-1)!. \qquad [7]$$

The density function $f(\tau)$ desribes the transit times of individuals $\tau_1, \tau_2, \ldots, \tau_n$ through the distributed delay process. The mean and variance of the random variable τ are respectively,

$$\mu_\tau = DEL \qquad [8]$$

$$\sigma_\tau^2 = DEL^2/k. \qquad [9]$$

In the limit as $k \to \infty$, the probability density function $f(\tau)$ approaches a normal distribution with mean DEL and zero variance. In modeling real-world problems, DEL and k can be chosen or estimated from time-series to approximate the properties of the process being modeled.

Manetsch (1976) has extended the concept of distributed delays to the case where the mean delay varies with time; these are referred to as time-varying distributed delays (TVDD). Using weather data which normally contains daily maximum and minimum temperatures, a continuous temperature profile T(t), can be constructed using the "sine-curve method" (Baskerville and Emin 1969). Thus, equation 6 or developmental velocity curves can be used to compute the instantaneous maturation delay, DEL(t). With this instantaneous delay, DEL(t), and a chosen value for k, the time-varying distributed delay can be used for modeling insect development. A generalized delay is included as an inset in Figure 20.

Population models can now be constructed linking TVDD's in series and providing survival coefficients either during the delay process or at the end of each instar. This technique constitutes the basis for discrete component phenology models and, ultimately, the aggregate system model.

PHENOLOGICAL MODELS IN THE ETC-FWW SYSTEM

Phenology models are an important aspect of any population study for many reasons. Their main contribution lies in the insight gained in host-parasite and herbivore-plant synchronies. In addition, they are essential in the timing of population samples and other field oriented activities. In the following section, each component of the defined system will be described with reference to its placement in time and some factors governing this placement. The individual components will also be related in terms of direct relationships with other components. Thus, developmental rates and patterns of mortality are discussed for the ETC and FWW. In turn, each is related to significant events in WBC phenology.

Leaf Growth in Wild Black Cherry

Leaf expansion in WBC begins at approximately 65 D-D_9*, considerably earlier than the majority of other deciduous trees occupying the same

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*Because there are no empirical data available for the determination of a developmental threshold, 9° C will be used because of the close association with the ETC (see Appendix C).

habitat. Expansion continues in a linear fashion for the next 300 D-D_9 peaking at 400-500 D-D_9 (Fig. 4). This peak marks the end of the major leaf growth period. The second phase of leaf phenology is marked by a significant decrease and leveling off coinciding with the flowering period and an initial drop of some of the larger leaves. Additional leaves are added at this time (Fig. 4, pt. A) which have the effect of lowering the mean leaf area but increasing total surface area (i.e., A x No. leaves). The end of this period is marked by fall leaf drop and a concurrent decrease in the mean and total leaf area (Fig. 4, pt. B, ca. 1200 D-D_9).

There are a number of factors which contribute to the variability in the rate and timing of the above phases of leaf phenology. I have already mentioned that the number of leaves dropping from larger size classes has an effect. In addition, temperature and precipitation would be hypothesized to exert a significant effect on leaf area in WBC. Independent variables which may influence leaf area include: cumulative D-D_9's, incremental D-D_9's between sample points, incremental precipitation, precipitation per incremental D-D_9, and number of leaves per branch. A forward step-wise multiple regression was used on $\log_e$ transformed data for 1977 and the following variables proved significant: precipitation per D-D_9, cumulative D-D_9's and number of leaves per branch. These results verify the original hypothesis. However, problems with multicolinearity restrict the use of cumulative D-D_9 and number of leaves, with a Pearson correlation of -.9419. In the final analysis only cumulative D-D_9's are used along with precipitation per incremental D-D_9 due to a greater proportion of the variability being explained by degree-days alone (76.83% vs. 58.40%). In addition, leaves/branch applies only to those branches sampled whereas, cumulative D-D_9 have a more universal application. A summary of the

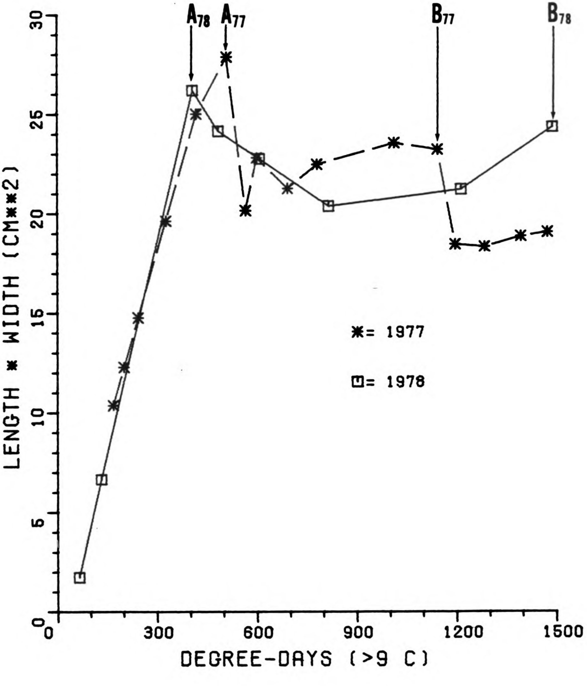


Figure 4. Relationship between mean leaf area and degree-day accumulations in WBC.

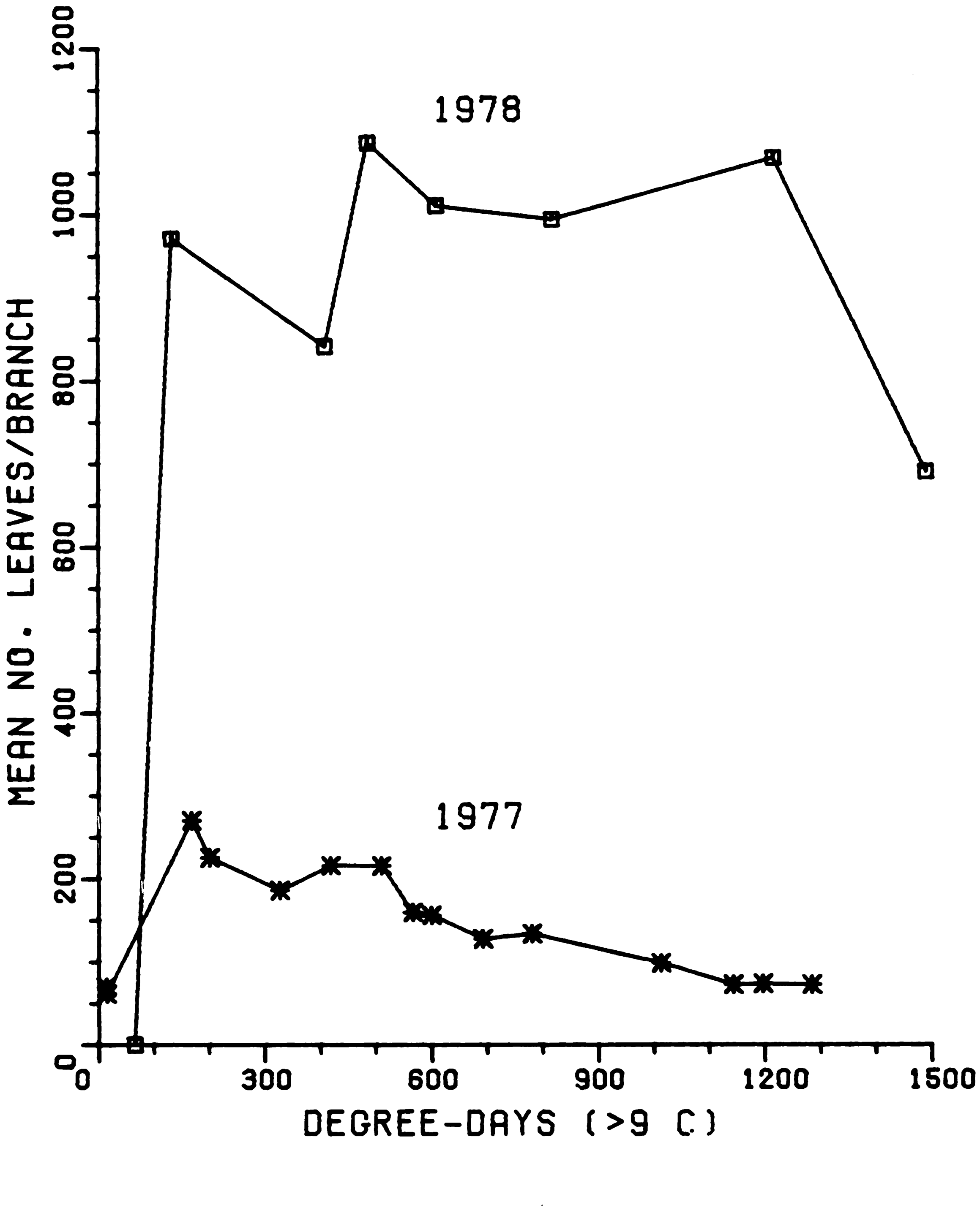


Figure 5. Relationship between leaves per branch and degree-day accumulations in WBC.

regression statistics is presented in Table 1 with the equation:

$$LxW = (2.3857)\ (CUMDD)^{.2106}(CMDD)^{-.1651} \quad [10]$$

where:

CUMDD = cumulative $D\text{-}D_9$'s, and

CMDD = centimeters of precipitation divided by $D\text{-}D_9$ during the sample period.

Analysis of 1978 leaf data provides similar results; however, increased precipitation produced no significant effects on leaf area (Table 1). The regression equation is:

$$LxW = (.1195)(CUMDD)^{.7847} \quad [11]$$

It appears that precipitation becomes a significant factor in leaf area when occuring in limited quantities (i.e., 1977). Throughout the 1978 season, rain occurred often enough and in sufficient quantities so as to produce no apparent growth effects on a within-season basis.

Table 1. Summary of regression statistics for WBC leaf area.

Variable	F to Enter	r^2	Overall F
1977 Leaf Area:			
Cum. Degree-Days	12.12***	.5026	12.12***
$CM/D\text{-}D_9$	12.62***	.7683	18.24***
1978 Leaf Area:			
Cum. Degree-Days	20.84***	.7764	20.84***

***$(p < .01)$

A generalized model. I will conclude this brief analysis of leaf growth by presenting a model of leaf area which summarizes and explains the observed patterns. There are 3 major stages to the phenology of leaf area in the WBC (Fig. 6A). Stage I is characterized by bud break and leaf expansion. During this period, leaf area due to leaf expansion (LA_E) is greater than the leaf area lost from the drop of large size class leaves (LA_D). Stage I ends with $LA_E = LA_D$ at approximately 500 $D\text{-}D_9$ (Fig. 6B). Stage II represents a quiescent period with $LA_D > LA_E$ due to no significant losses of leaves. Finally, there is an increase in LA_D (ca. 1200 $D\text{-}D_9$) or the fall leaf drop which continues until all leaves have been lost.

The model assumes that factors such as precipitation are not wanting. Were we to superimpose the findings of the regression analysis on this conceptual model, the rates of change in leaf area would be altered proportional to amounts of rainfall. Thus, the difference between LA_D and LA_E during State II and III would further be increased.

Phenology and Survival in the Eastern Tent Caterpillar

Egg and first instar phenology. During early summer (June-July), ETC adults emerge and deposit egg masses on the branches of WBC and other roseaceous host plants. Within 2-3 weeks pharate first larval instars are fully formed and undergo obligate diapause. Diapause or quiescence for pharate larvae continues until the following spring. Egg hatch begins very early in the season at approximately 20 $D\text{-}D_9$ and extends over a 100-140 $D\text{-}D_9$ period peaking at 65 $D\text{-}D_9$ (Fig. 7). The distribution of egg hatch was derived under laboratory conditions and thus serves only as an initial model for field verification. This was done by observing egg

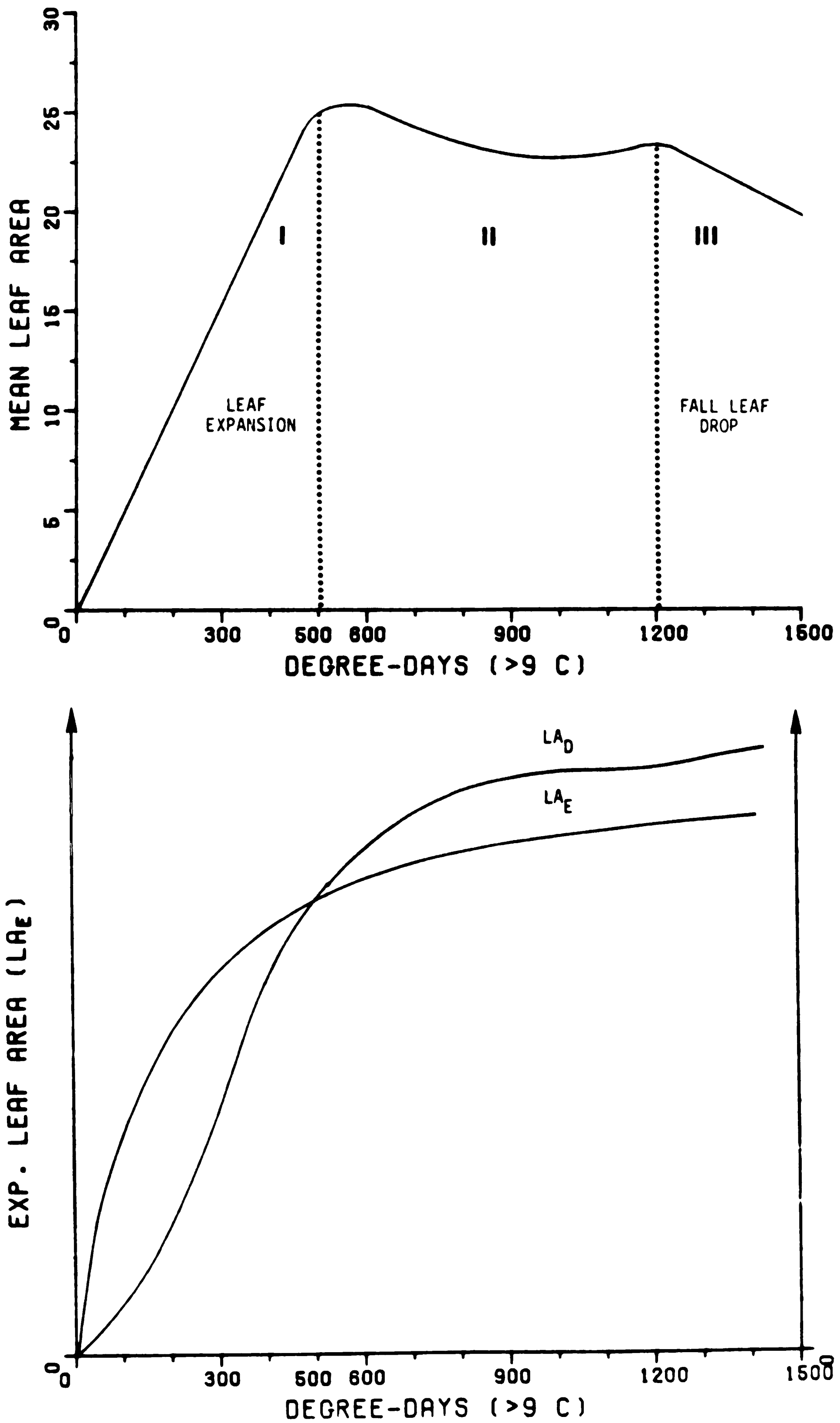


Figure 6. Qualitative phenology model for leaf area in WBC.

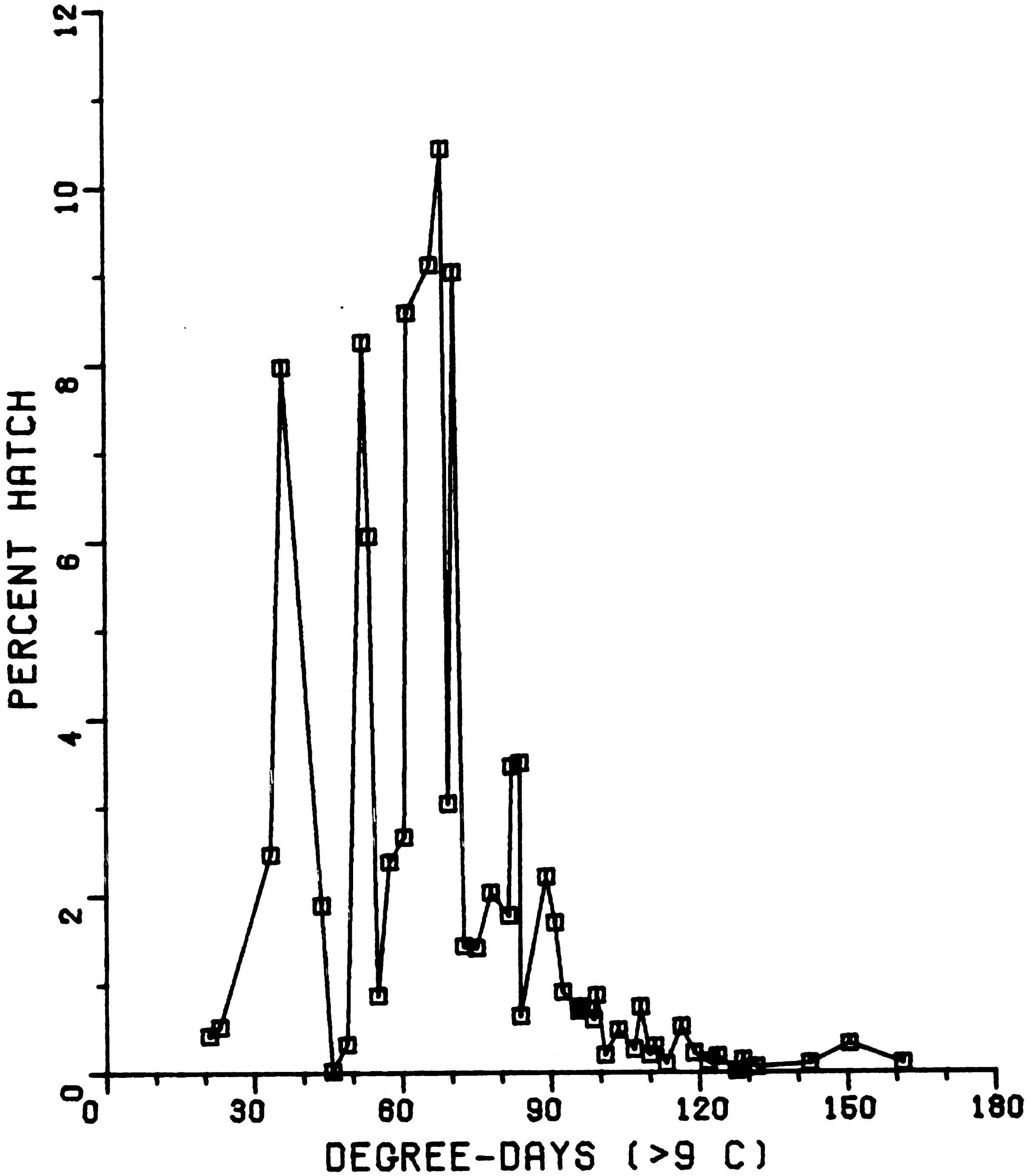


Figure 7. Distribution of degree-days required for ETC egg hatch.

masses under field conditions and recording whether or not at least one larva had emerged. In this context, 100% emergence indicates that all egg masses had begun to emerge. The cumulative emergence curve for the laboratory population shows that all egg masses initiated emergence by 65 D-D_9 or approximately 50% of the total larval population (Fig. 8). Under field conditions the point of 100% initial emergence occurred also at 65 D-D_9 (Fig. 9, curve H).

Within the first 2 days after emergence (ca. 5-10 D-D_9) larvae form a silken mat on the surface of the egg mass and remain there for an additional 5-10 D-D_9. After this silking and resting period, the colony moves to an adjoining fork of the tree to begin tent formation. The relationship between these 3 activities is shown in Figure 9. The lag in tent formation and initial decrease in larval activity is further demonstrated in the differences of the rates of hatch and tent building. If larvae were able to silk and form tents at the same rates as hatching, then we would expect the T and S curves in Figure 9 to mirror the hatch (curve H). Larvae are initially able to hatch at a rate of 1.12%/D-D_9, whereas tent formation is lagged by at least 5 D-D_9 and increases at .27%/D-D_9. Once the population has begun to produce significant numbers of tents, increased variability tends to decrease the rate of tent formation in relation to hatch rates. Analagous portions of H and T curves may be compared with rates of 6.36%/day and 4.78%/day, respectively.

Possibly one factor adding to increased variability is sample bias. After 50 D-D_9 bias enters the calculations. Samples taken during this time favor those colonies forming tents due to visual bias of the sampler, causing proportionately more tents to be observed than unhatched egg masses and further decreasing the T slope.

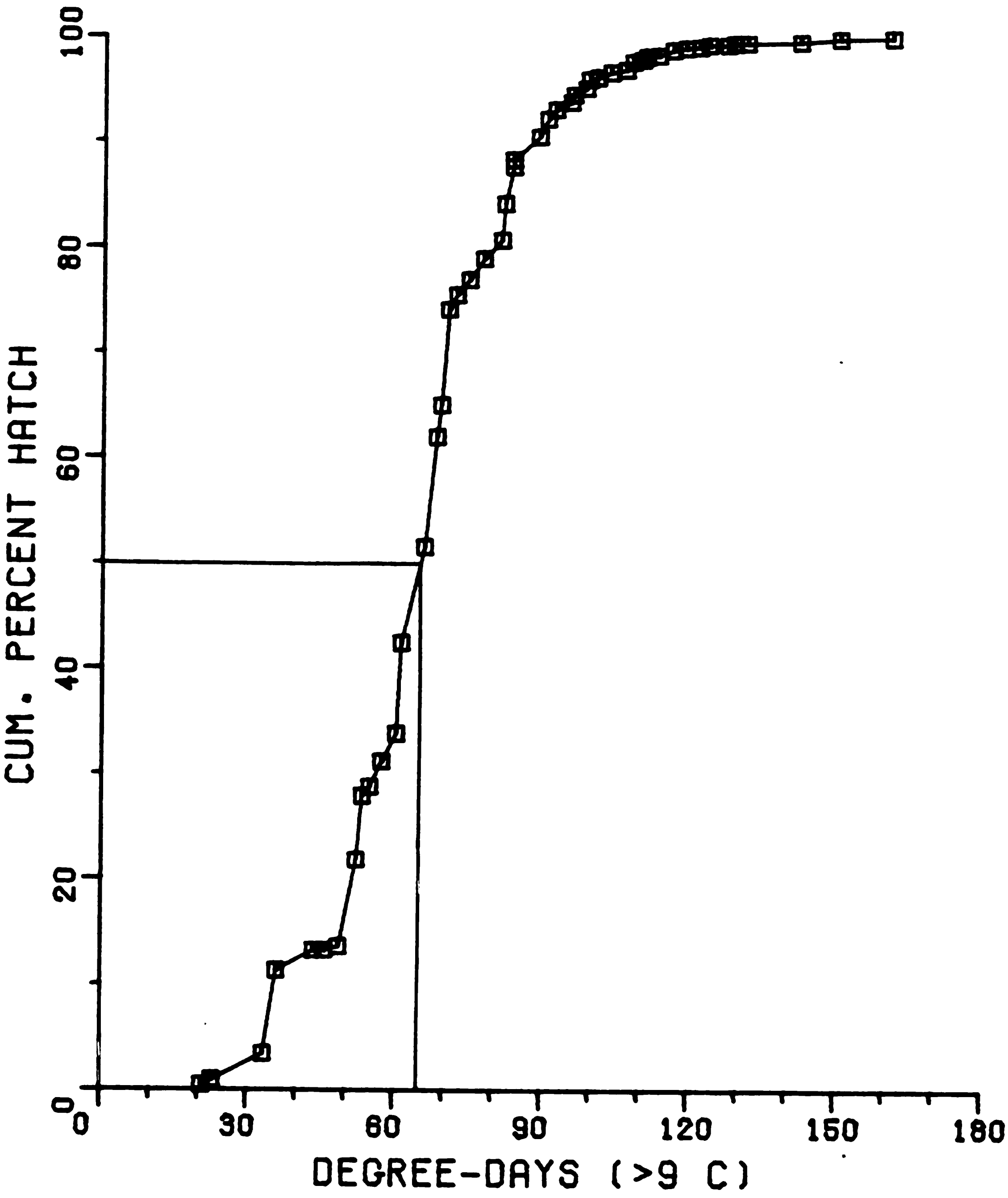


Figure 8. Cumulative distribution of ETC egg hatch indicating the 50% mark.

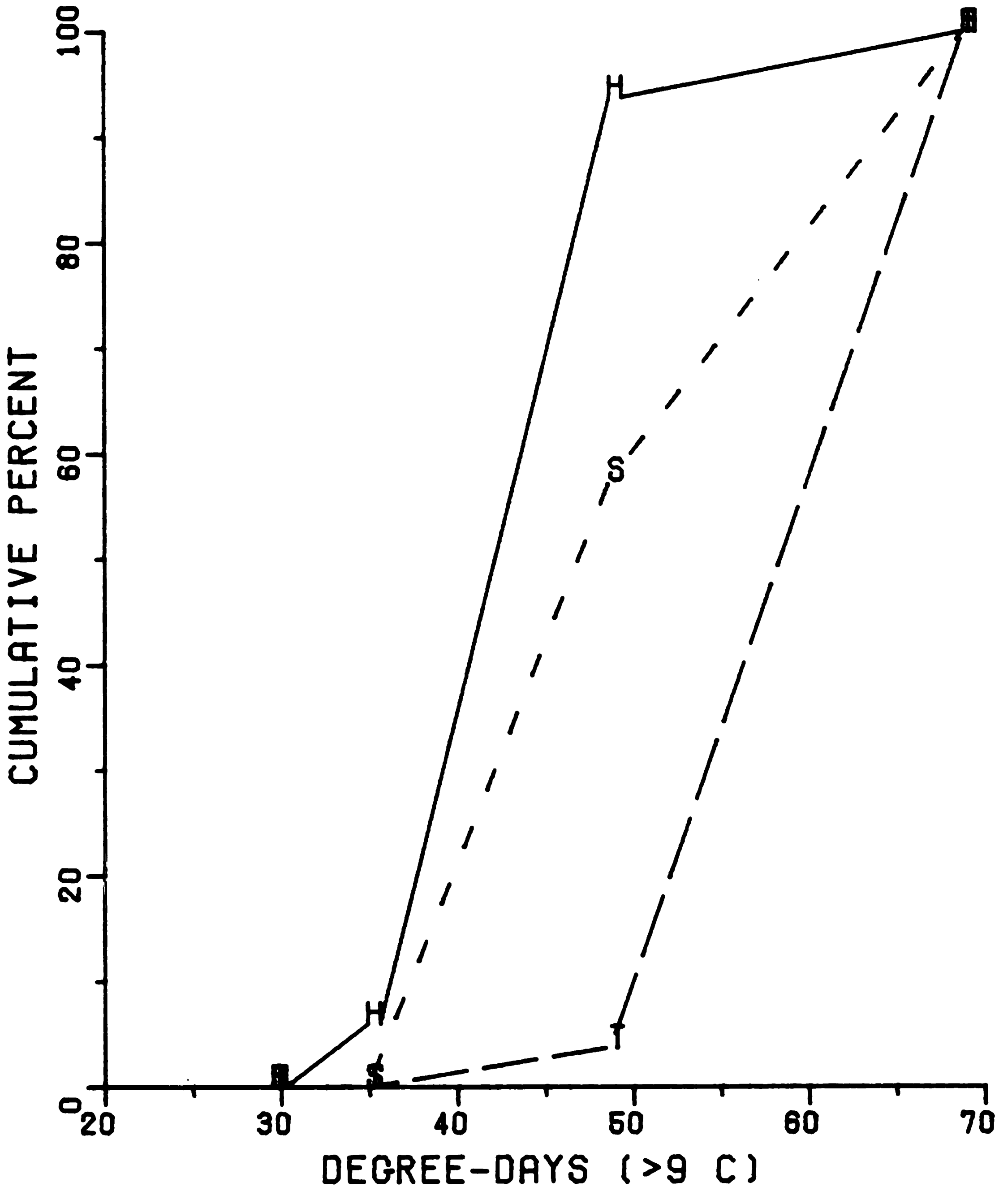


Figure 9. Field relationships of ETC egg hatch, larval silking and tent formation.

Following tent formation it is of utmost importance that first larval instars are well synchronized with the succulent high quality buds of WBC. This is due to the fact that larvae which are forced to feed on fully developed leaves have an extremely difficult time piercing leaf tissues. Further, those that are successful in consuming foliage are unable to do so at a rate comparable to bud feeders. At least 1 individual from every egg mass (50% of the total hatch) emerged during the bud stage with only 33% of peak leaf expansion completed at 100% hatch (Fig. 10). Of 150 egg masses placed on trees in early June only 53% of the colonies were able to establish themselves compared with over an 80% success rate for normal masses (April). Admittedly, there are other factors acting on ETC masses at that time; however, laboratory larvae placed on fully developed leaves in the spring produced only slightly better results. These findings support the idea that ETC is highly dependent on the quality of the foliage.

Leaf growth and larval maturity. In most cases temperature is used in driving phenological models, and thus population phenomena are viewed as a function of heat unit accumulations (D-D). This is desirable for making predictions concerning timing of samples due to availability of temperature data. On the other hand, on-site measurements are not always possible. Thus, it might be expedient to utilize the plant as an integrator of aggregate weather conditions, assuming that the "pest" and plant are highly correlated in their development.

Throughout the ETC egg hatch period it was shown that there is a close association between bud and leaf development and the rate that first instars enter the field. In fact, overall larval development is highly correlated with Stage I of the WBC phenology (Fig. 6). The ETC requires

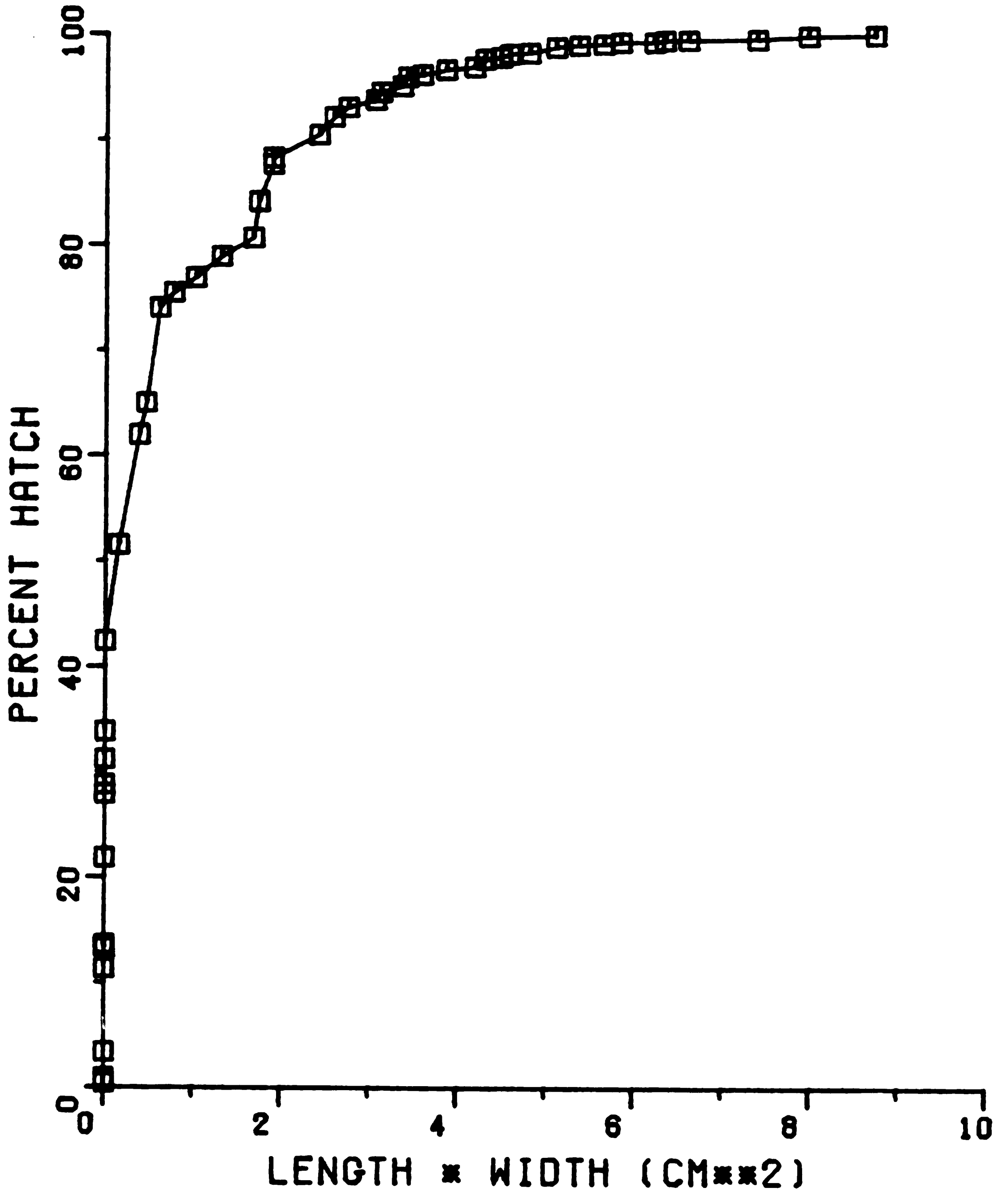


Figure 10. Relationship between ETC egg hatch and leaf area of WBC.

approximately 400 D-D9 to complete larval development. Similarly 400-500 D-D9 are required for maximum leaf expansion in Stage I.

In order to utilize WBC leaf growth in a predictive mode we must also have a suitable measure of population maturity in the tent caterpillar. Population maturity may be measured in a number of different ways. One of the most common measures is the mean larval instar (MLI). The MLI is defined as:

$$\mathrm{MLI} = \sum_{i=1}^{k} N_i i / \sum_{i=1}^{k} N_i, \qquad [12]$$

where:

N_i = the number of larvae in the i^{th} instar with a total of k instars.

The major problem with the MLI is that it assumes that equal portions of time are spent in each instar. An alternative measure is the weighted mean instar (WMI) which takes into account differences in instar length. Specifically it includes the proportion of the total larval period spent in each instar (p_i) or:

$$\mathrm{WMI} = \sum_{i=1}^{k} N_i i p_i / \sum_{i=1}^{k} N_i p_i \qquad [13]$$

(Fulton 1978).

Regressing the WMI ($\log_e$ transformed) for 1977 as a function of leaf area ($\log_e$ transformed) produces a significant relationship ($p < .01$) with the resulting equation:

$$\ln(\mathrm{WMI}) = -1.452 + 1.094[\ln((L\mathrm{x}W)+1)] \qquad [14]$$

$$r^2 = .9218.$$

Data from 1978 can now be used to verify this model by direct comparison of regression lines. The equation for 1978 data is:

$$\ln(WMI) = -.6151 + .8020[\ln((LxW)+1)] \qquad [15]$$

$$r^2 = .8868.$$

Regression lines were compared using a t-test for a common β (Steel and Torrie 1960). Significant differences in the slopes of the lines were obtained ($t = 8.069$, $p < .01$) (Fig. 9). This was not entirely unexpected due to precipitation effects on leaf area, as described earlier (Table 1). An additional factor creating differences in slopes is possible differences in developmental thresholds and/or rates of development. In 1977 D-D accumulations began February 23 and continued to March 15 with a total accumulation of 25 D-D_9. After that, a cold period continued for 10 days in which there was no heat accumulation. Under normal circumstances ETC hatch would have begun at that time but at very low levels (< 1%). Significant hatch in the field did not occur until the 55 D-D_9 mark or 20 D-D_9 after the cold period. It would appear then that ETC hatch had, more or less, been "reset" and that an additional 20 D-D_9 were required for first instar emergence. This is a feasible hypothesis in that first instar development is completed during the first month after egg deposition. Therefore, the developmental threshold concept is not applicable in this case. Rather a hatching or activity threshold may have more validity for spring hatch of ETC eggs. The tree, on the other hand, was able to begin bud break and leaf expansion causing some asynchrony with 50% larval emergence and bud break (Fig. 10).

Adjusting the 1977 data by 25 D-D_9 (i.e., subtracting 25 D-D_9 of development from the LxW) produces a new equation:

$$\ln(WMI) = -.9492 + .9385[\ln((LxW)+1)] \qquad [16]$$

$$r^2 = .8826.$$

Even with this adjustment the 2 regression coefficients proved to be significantly different, though much less so ($t = 4.05$, $p < .01$).

The above analysis has shown that significant differences in herbivore-host synchrony may occur between years due to temperature and precipitation. Because of these differences and lack of substantial data concerning the WMI-LxW relationship, a precise model cannot be formulated at this time. On the other hand, estimates of WMI can be obtained which have considerably wider confidence limits but still provide at least preliminary prediction. Combining both years data produces the model:

$$\mathrm{WMI} = (.15198)(\mathrm{LxW}+1)^{.8026} \qquad [17]$$

$$r^2 = .8717.$$

Figure 11 shows this relationships and includes the 95% confidence limits on WMI.

Along with the regression models which have a plant orientation, a simulation model was developed. This particular model is temperature driven and may be used in situations where on-site data are available and predictions are required from a remote laboratory. Further, it appears that this model has considerably more repeatability on a year-to-year basis. Because this technique was extensively used in the development of the system model, I will defer discussion of those results to a later section.

Survival in the eastern tent caterpillar. There are 2 ways in which survivorship in organisms is viewed. First, the number of individuals occurring per unit area over the length of a generation can be transformed into a distribution of probabilities over time resulting in a survivorship curve. This technique has the advantage of viewing survival as a continuous process and provides a graphic representation of the pattern of survival.

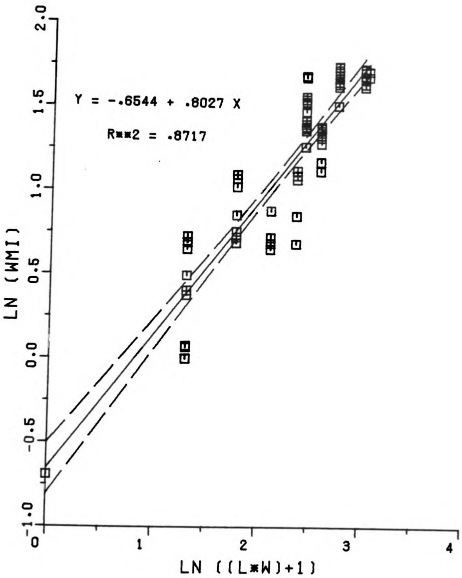


Figure 11. Relationship between ETC weighted mean instar and leaf area.

The second approach, life tables, involves survivorship as it pertains to any particular life-stage or group of life-stages. This method provides survival coefficients which are utilized in subsequent analyses (i.e., models). In either case, one may determine what life stage or points in time are particularly susceptible to mortality.

The distribution of mortality. Survivorship in the ETC may be described as a combination of 2 theoretical generalized curves. A Type I curve restricts the majority of mortality to the latter stages of life, and Type III to the earlier stages (Price 1975).

We may begin by first examining egg mortality. Eggs are laid early in the summer and remain in that stage until the following spring. In actuality, complete development of first instar larvae occurs within the first month after oviposition (Mansingh 1974). However, for the purposes of this discussion they will be referred to as eggs. With approximately 80% of their life spent in the egg stage one would suspect it to be highly resistant to the rigors of the environment. This appears to be the case with a mean survival rate of .8425 ± .0440 over the 4 years in which data were available. No appreciable mortality could be attributed to weather effects, parasitism or predation, and no significant differences were detected from 1976 through 1979 (Fig. 3.12) ($P < .05$). An additional hypothesis is that as the number of eggs laid increases, the quantity and quality of yolk for the developing embryos decreases. Pooling the 4 years of egg mass data it was found that this is not the case. Concurrent with the above hypothesis, a significant negative slope would be expected with respect to percent survivals as a function of eggs/mass. No significant density dependence was detected with a constant positive slope of 0.9430 (Fig. 13).

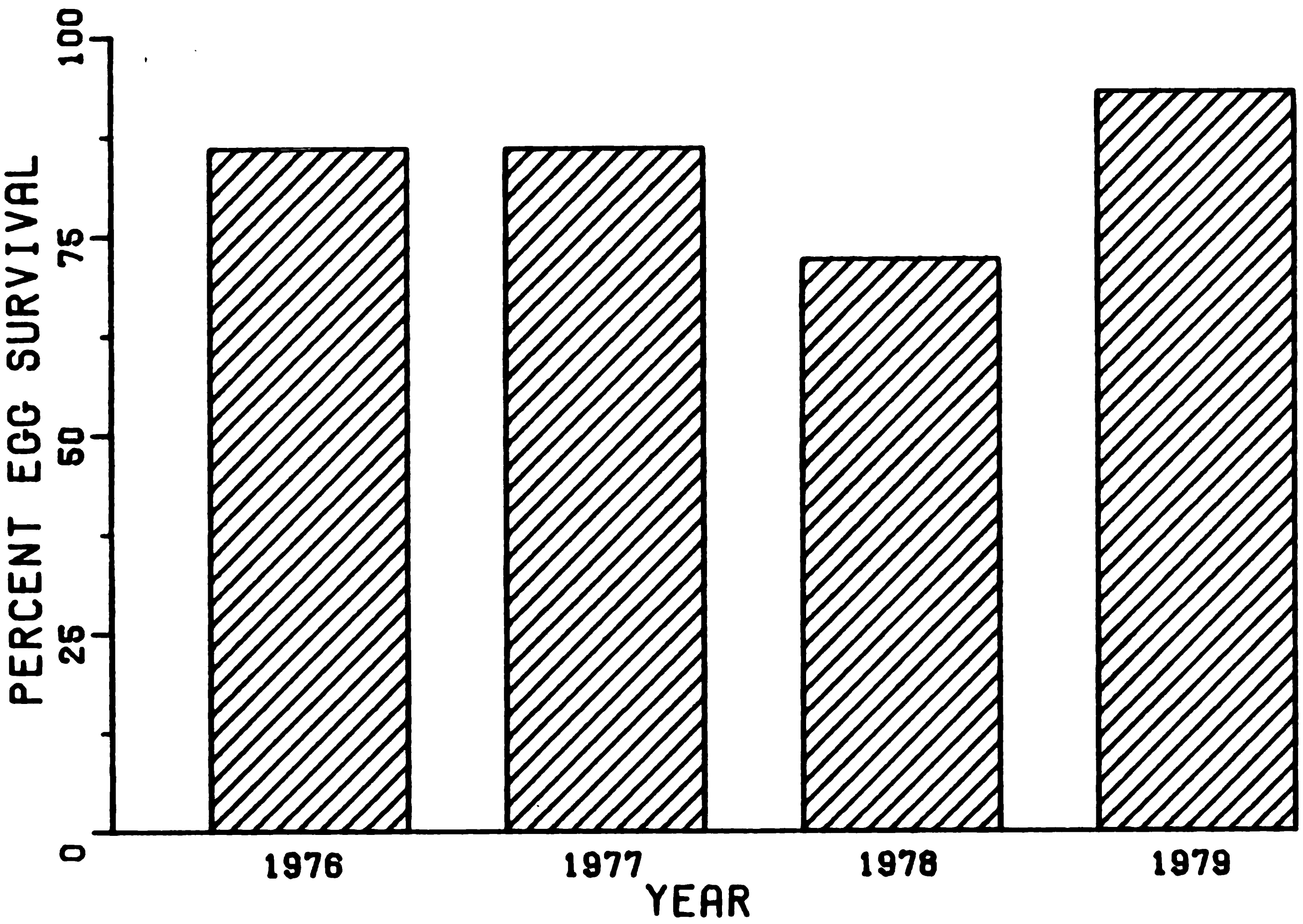


Figure 12. Percent ETC egg survival for Gull Lake, Michigan, 1976-1979.

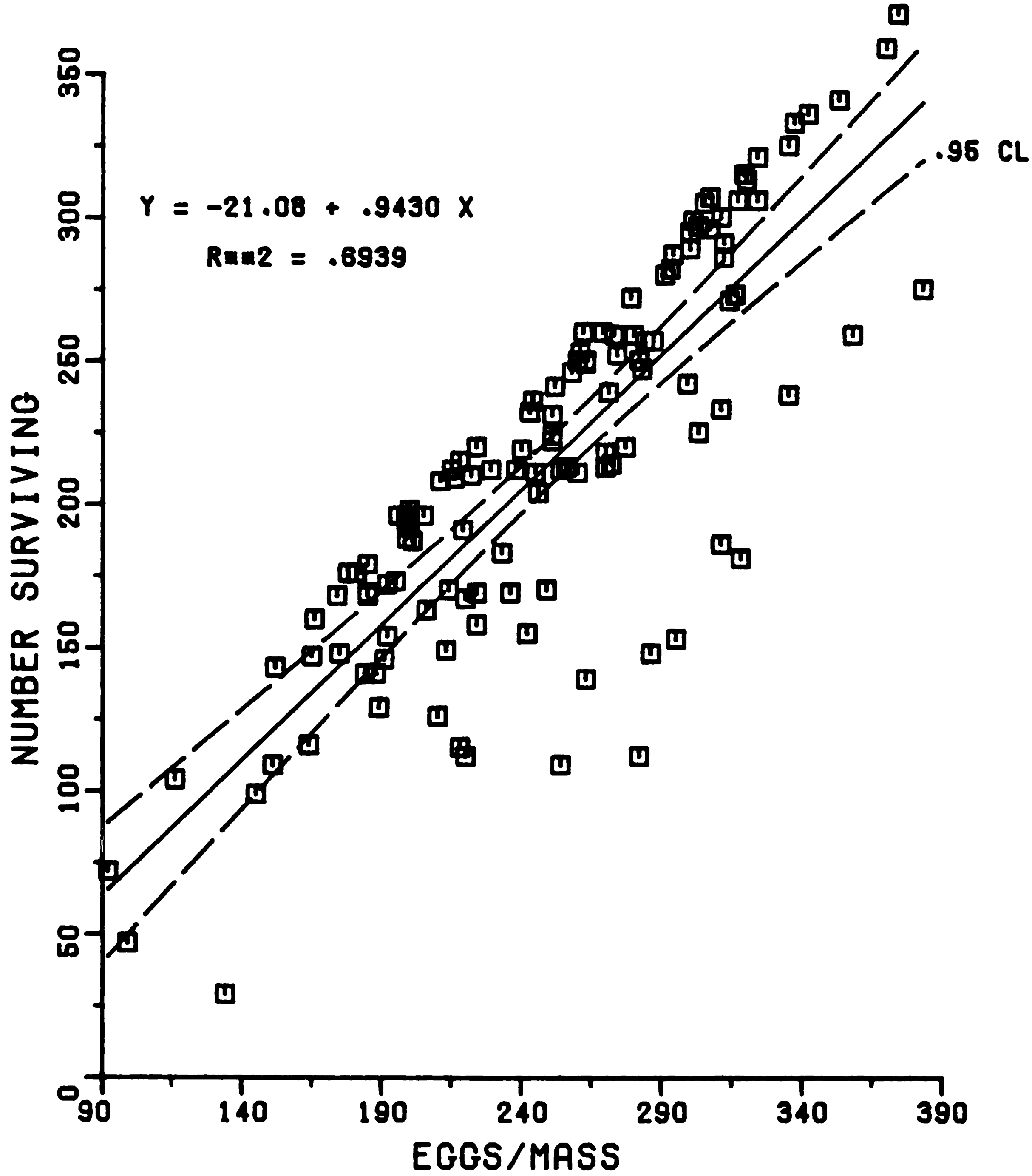


Figure 13. Relationship between eggs per mass and ETC egg survival.

Immediately after eclosion and just prior to tent formation, ETC first instars are susceptible to a number of mortality factors. Yet, throughout the course of this study only 5-10% additional mortality was detected after egg hatch. Much of this mortality may be attributed to attacks by ants. Studies indicate that foraging by ants such as *Formica obscuripes* Forel is a common phenomenon. Further, this foraging is coincidental with bud break and extrafloral nectaires which are active during this period (Tilman 1978). This would also be correlated with peak ETC hatch at approximately 65 D-D_9 as derived from historical records and dates recorded by Tilman. Tilman's data suggest that ant predation is patchily distributed and dependent on the proximity of ant colonies to ETC colonies. Thus, it appears that the effects of predation will be felt on a localized basis and would not affect regional population significantly.

Once the colony has been able to form a tent the rate of mortality levels off, and by 150 D-D_9, 70% of the colony is still intact. By 200 D-D_9 feeding and general activity has increased considerably. Older life stages (instars 5-6) appear in the colonies and greater amounts of mortality are realized. At this same time the WBC has ended Stage I, bloom has taken place, and the quality of the foliage has begun deteriorating (Fig. 6). Thus, between 150 and 200 D-D_9, survival rates drop from 70% to 55%. Sixth instars are prevalent within colonies and begin to move out on the foliage, drop to the ground, and disperse toward pupation sites.

Figure 14 shows the number of individuals remaining in the colony over a 400 D-D_9 period. For one-half of the 400 D-D_9 the proportion remaining is equated only with survival. However, once prepupational dispersal begins at 200 D-D_9 the sampling technique used (tent samples)

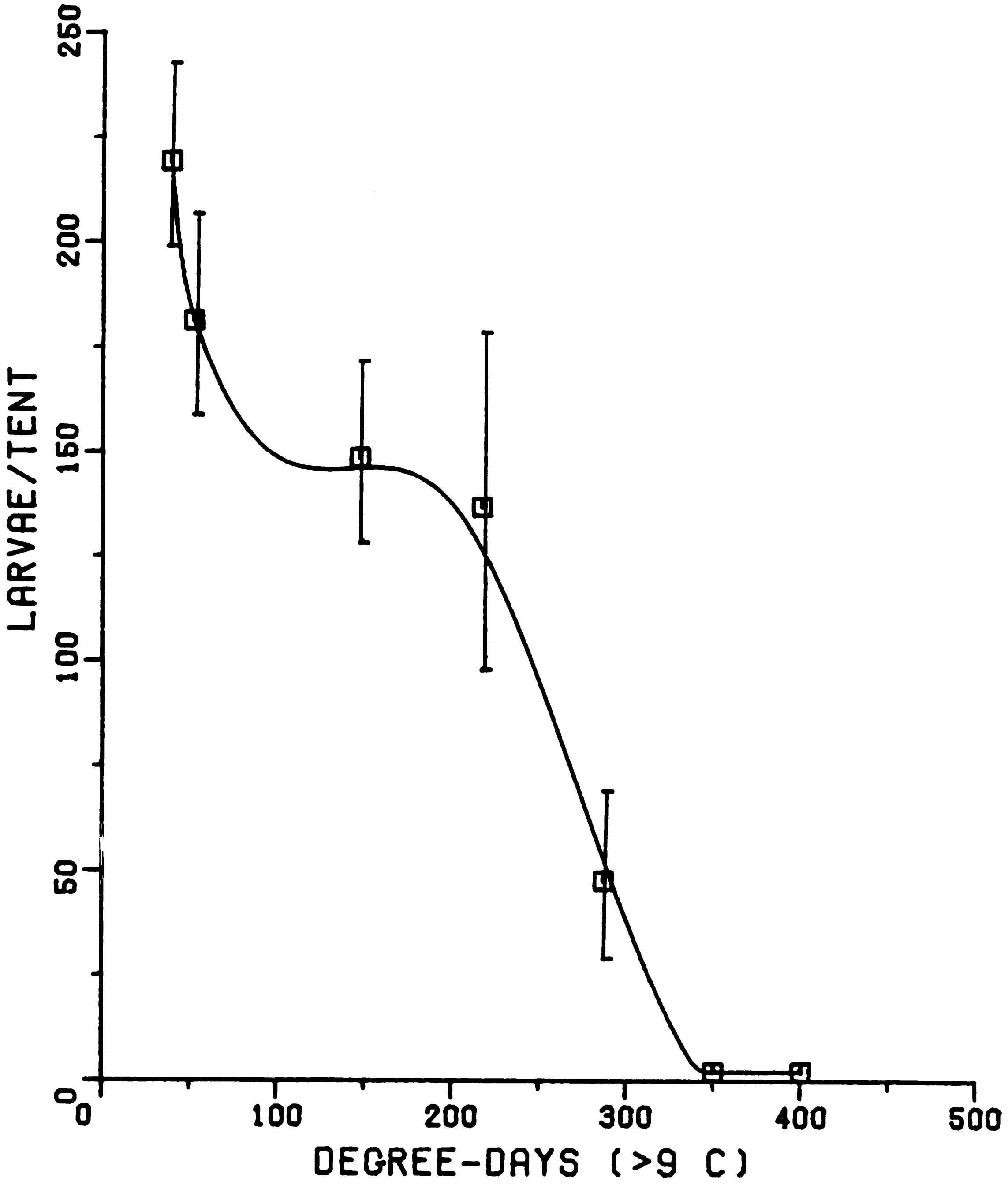


Figure 14. ETC larvae per tent (± .95 C.L.) in relation to cumulative D-D_9.

becomes confounded with 2 processes: survival and dispersal. Thus, the later part of the curve represents the probability of surviving (P_S) and the probability of dispersing (P_D) at that point in time. The probability of still remaining in the tent (P_R) is therefore:

$$P_R = (P_S)(1-P_D). \qquad [18]$$

Knowing P_D allows a calculation of P_S as it relates to survivorship *within* the colony or:

$$P_S = P_R/1-P_D. \qquad [19]$$

P_D was estimated in the field by placing large sheets of plastic beneath 9 trees with single ETC colonies. The perimeter of each sheet was raised so as to form a funnel-like collection device for dispersing larvae to fall into. Collections were made, for the most part, on a daily basis. Figure 15 shows the cumulative percentages or probability of dispersing, P_D. Survivorship curves can now be corrected for dispersal through equation 19 and plotted (Fig. 16). The estimates obtained may slightly overestimate survival. This is due to individuals which have died and fallen into the collection "funnel" being counted as dispersing larvae rather than expiring.

Looking at the overall pattern of survival it appears that the tent affords an extreme amount of protection for ETC larvae. The first 100 D-D_9 is spent in the hatching phase with a 20% reduction in the colony (Fig. 16A, pt. A). Once tent formation has occurred little mortality takes place; approximately 10%. From the point where sixth instars first start appearing in the colony (pt. B) until the end of prepupational dispersal, an additional 45% of the colony is lost. This would indicate that with larger instars spending greater amounts of time away from the tent or

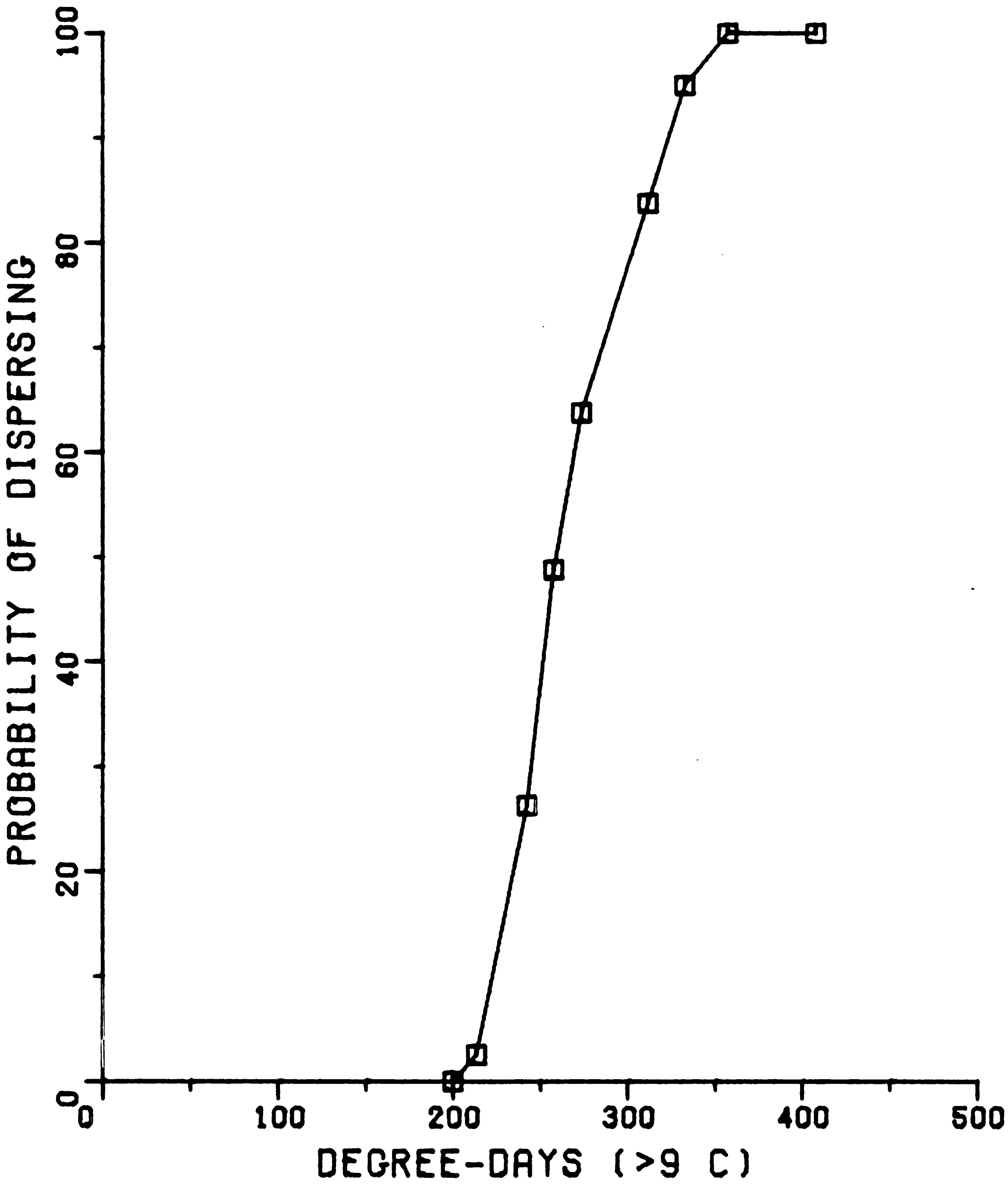


Figure 15. Probability of ETC larvae dispersing from the colony.

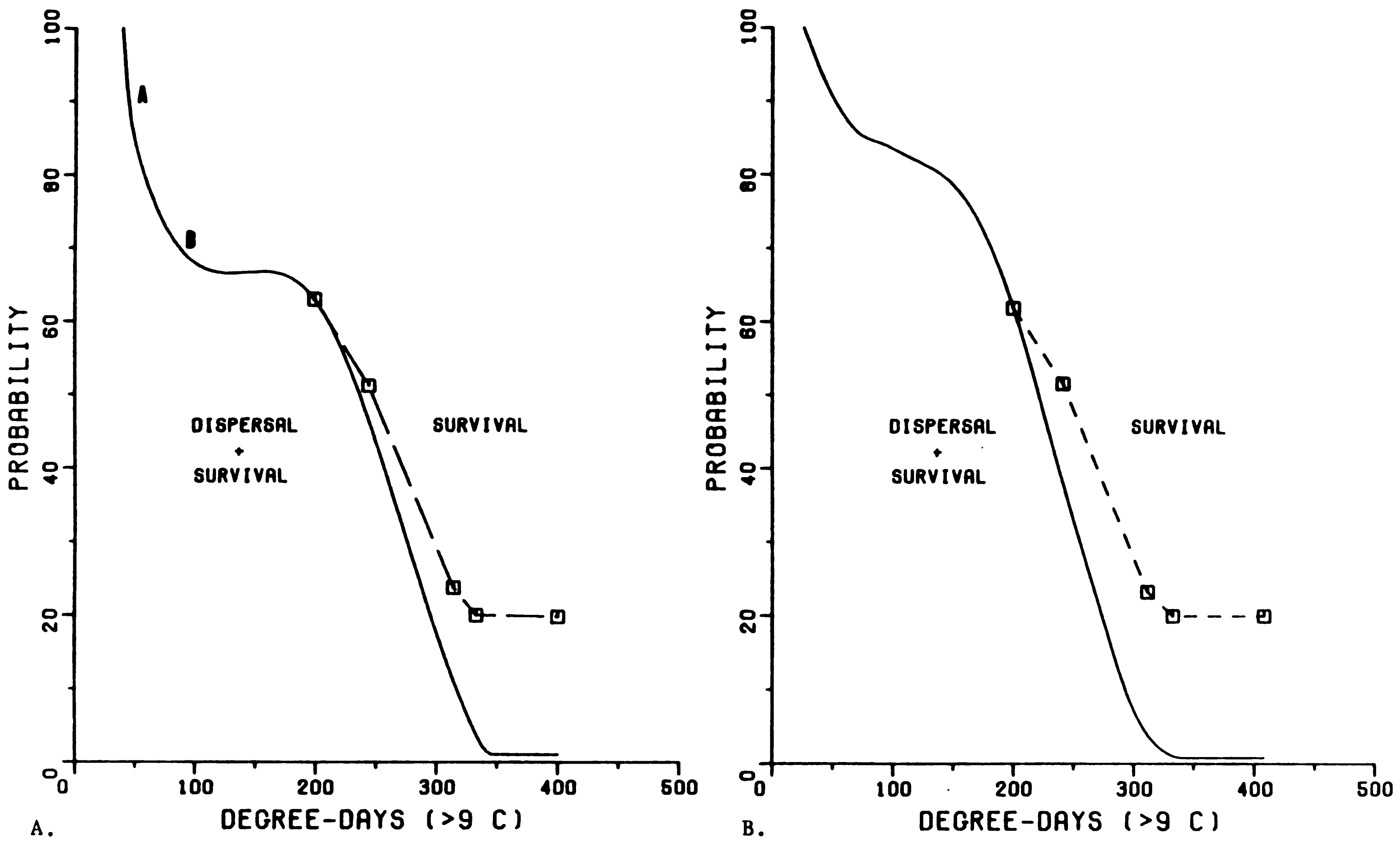


Figure 16. Probability of ETC larvae remaining in the colony due to dispersal and survival.

on its surface, factors such as predation, parasitism, and weather variables have a much greater chance of affecting ETC larvae. Thus, 65% of the mortality occurs while larvae are either building the tent or foraging away from its confines.

Stage-specific survivals. Once again, the pattern of survival described above emerges with the majority of mortality in the very early stages and the very late stages (Table 2). Instars 3 and 4 were combined in 1978 due to poor timing of samples missing a significant portion of the third instar. For purposes of comparison these instars were also combined for 1977.

Determination of fifth and sixth instar survival presents a problem due to the tent-oriented sampling technique and the dispersal behavior of sixth instars. An approach to this problem was to take quadrat samples at the soil's surface to collect any dispersing larvae or pupae. In addition, emergence traps were placed in the field to determine adult densities. Unfortunately, neither technique proved adequate. One-hundred quadrat samples ($1m^2$) were taken in each subplot for the 3 study areas (1500 samples) in 1977 producing a survival rate for instars 5 and 6 of less than 1%. This rate seemed unreasonably low with 50 emergence traps producing a similar result for instars 5-P. The only recourse was to utilize the fact that ETC females deposit only one egg mass. Late stage survival was then calculated from the number of colonies in the following season which was equated with the number of surviving females in the present season. This produced an aggregate survival including instars 5 through adult, as well as any immigration or emmigration. Rates of .0544 and .0413 were calculated for 1977 and 1978, respectively.

Table 2. Life-tables for the eastern tent caterpillar.

Age Interval (X)	No. Alive at at the Beginning of X (N_x)	No. Dying During X (M_x)	M_x as Percentage of N_x	Survival Rate Within X
1977:				
Eggs	219.41	38.06	17.35	.8265
Instar I	181.35	0.036	0.02	.9998
Instar II	181.31	7.56	4.17	.9583
Instar III	173.75	39.82	22.92	.7708
Instar IV	133.92	67.59	50.47	.4953
Instar III-IV	151.49	96.07	63.42	.3658
Instar V-A	66.33	62.72	94.56	.0544*
1978:				
Eggs	218.38	33.00	15.11	.8489
Instar I	185.38	22.65	12.22	.8778
Instar II	162.73	26.00	15.98	.8396
Instar III-IV	136.63	77.23	56.52	.4348
Instar V-A	59.40	56.95	95.87	.0413*

*Calculated from the number of tents in the following year equated to the number of emerging females in the present year (see text).

Phenology and Survival in the Fall Webworm

Studies involving population processes in the FWW have been done principally in Canada and Japan. Canadian researchers have centered on the idea of genetic control of fitness responses such as fecundity and larval and pupal survival. These fitness responses are highly correlated with the length of the pupal stage, symbolized as Kp (Morris and Fulton 1970a,b). Kp has been shown to vary, both between geographic locations and between years. Because of this, the so-called "quality" of any given webworm population will be exemplified by the frequency distribution of Kp. This frequency distribution is, therefore, a changing entity responding primarily to factors which act on large portions of a population such as temperature. Shifts in the distribution (fitness) may occur as a function of heat unit production (degree-days) for a given location in a given year. In years which exhibit extremely short and/or cool summers individuals with high Kp are suppressed due to the inability to accumulate sufficient heat units for pupation. Since diapause is restricted to the pupal stage, groups of individuals caught in these circumstances suffer high rates of mortality. Conversely, groups with high Kp are favored in extremely warm and/or long summers. Reduction in fat stores after pupation suppresses low Kp cohorts in this instance, as they will spend more time in the ground at high temperatures. This, in turn, reduces fat stores and has significant effects on pupal weight, fecundity, and survivorship (Morris and Fulton 1970a). The average fitness or quality of the population is then a function of the total heat available in the field and the history of the population determining heat requirements. The population of FWW occurring at Gull Lake, Michigan exhibits many of the characteristics described above. The mechanisms, on the other hand, are not necessarily restricted to temperature.

Synchrony of the FWW larvae with Stage II of WBC phenology is extremely important, as food quality degrades rapidly throughout the larval stages. In terms of the WBC, the webworm's oviposition period occurs in Stage II and larvae feed in Stages II and III (Fig. 6). The time of adult emergence (K_p) and oviposition will therefore, determine the type of foliage available to a webworm colony. Larvae which are forced to spend significant amounts of time in Stage III will be exposed to very low quality food and experience reductions in overall fitness. Morris' (1967) study of the effects of foliage age on survival and fecundity quantitatively demonstrates these effects. Larvae reared on early and mid season foliage produced no significant differences in larval and pupal survival. However, larvae reared on late season foliage had a 15 to 20% reduction in survival of larvae and pupae, respectively. Further, fecundity was affected by each treatment with early foliage producing a mean of 604 eggs/female, mid season foliage 372, and late 128.

Foliage age is not necessarily related only to degree-day accumulations. As pointed out earlier, foliage may "age" as a function of precipitation. Changes in the make-up of FWW populations in relation to WBC foliage quality would be expected.

The frequency distribution of Kp was calculated for 1977 and 1978. This was done through back-calculation from the weighted mean instar of each colony sampled, to the time of emergence (Fig. 17). Emergence for 1977 began at 618 D-D_{11} and continued until 1267 D-D_{11}. This is compared with 1978 where adult emergence began at 678 D-D_{11} and ended at 989. Referring once again to the WBC phenology, in 1977 it was found that significant changes in leaf area occurred at approximately 1100 $D\text{-}D_9$. Translating the degree-day accumulation (base 9) to the webworm threshold (base 11) it was found that these changes occurred at 949 $D\text{-}D_{11}$. If we accept Morris' data concerning genetic control of degree-day requirements and the fact that food quality affects larval fitness, then a truncation of the frequency distribution at 900-1000 $D\text{-}D_{11}$ would be expected. Both distributions began during the same time period (600-700 $D\text{-}D_{11}$) and have median values of 820 $D\text{-}D_{11}$ for 1977 and 809 $D\text{-}D_{11}$ in 1978. Therefore, the major differences lie in later portions of the 1978 curve. The 1978 data suggest that this is the case with the last adults emerging at 989 $D\text{-}D_{11}$.

Survivorship curves for 1977 and 1978 also demonstrate a shift in the webworm populations (Fig. 18). As much as 125 $D\text{-}D_{11}$ separate the 2 curves. However, it is not clear what other factors are contributing to changes in temporal occurence.

Because of the low levels of FWW at Gull Lake, a second population was sampled in Hartford, Michigan. The overall form of the survivorship curve bears a close resemblance to both of the Gull Lake curves. Differences between years and between locations then lie primarily in the placement of the population in physiological time.

No additional data are available to support hypotheses concerning frequency dependent changes in population make-up for Michigan. However, the sum total of each piece of information presented lends a more than feasible explanation to observed differences between years.

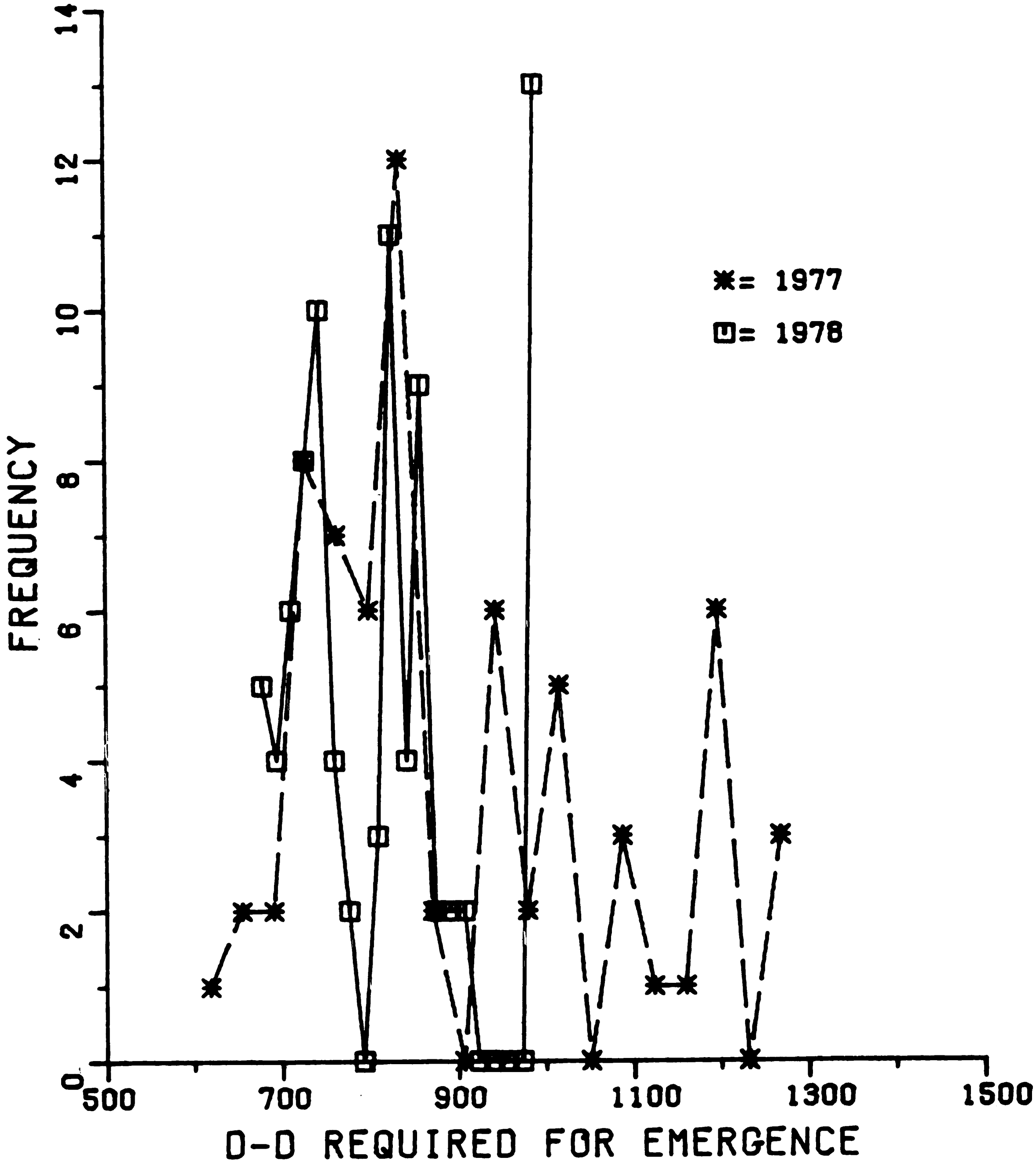


Figure 17. Frequency distributions of Kp for Gull Lake 1977 and 1978.

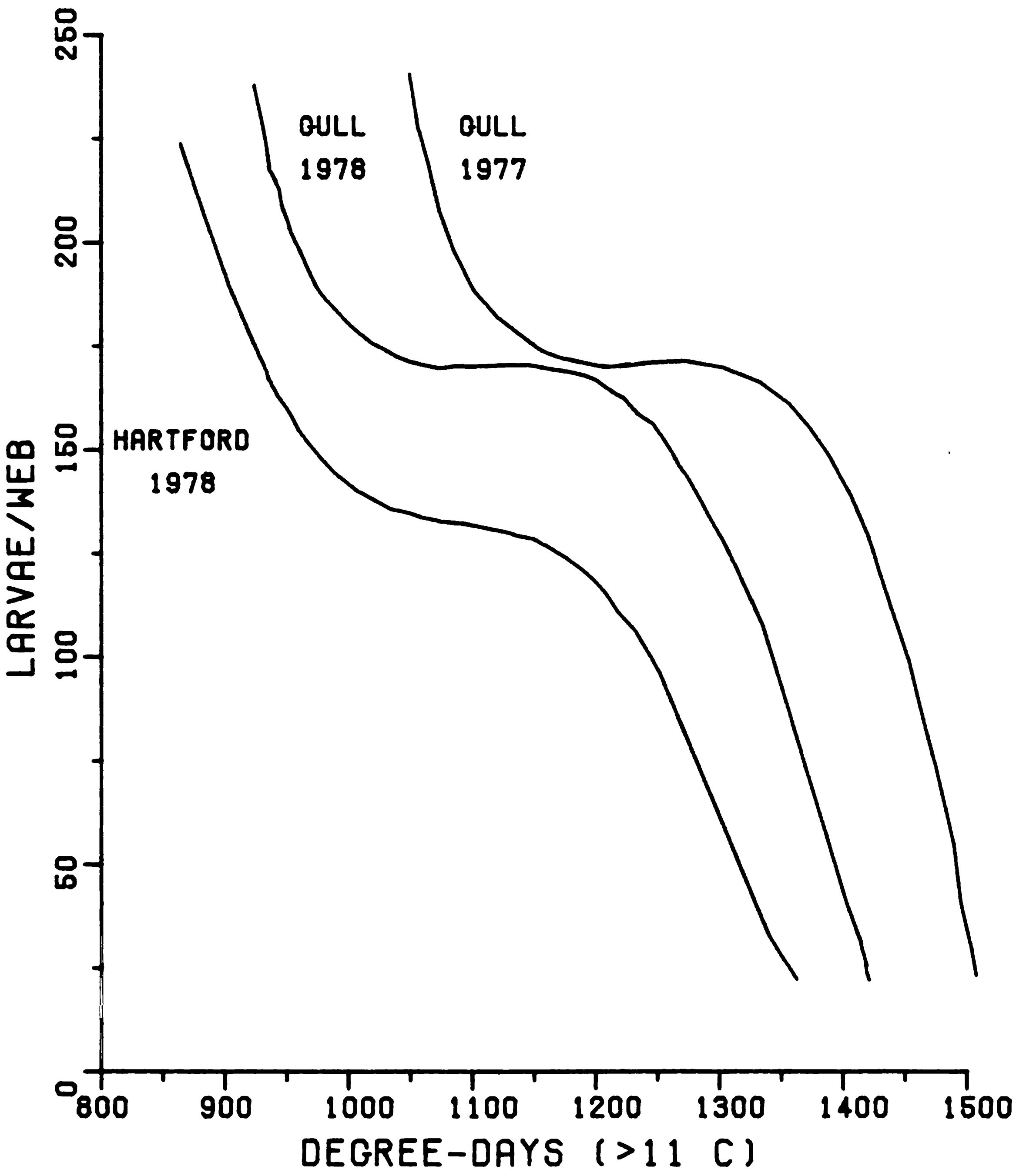


Figure 18. Survivorship curves for Gull Lake, 1977-1978 and Hartford, Michigan, 1978.

The Parasite Component

It was hypothesized earlier that *C. validus* was a likely candidate for inclusion into a more simplified system (Fig. 2). It attacked the ETC early in the year and the FWW later in the year. In addition, a sufficient amount of information was available with regard to attack rates and phenology. Throughout the 3 years of study at the Gull Lake research area *C. validus* was not detected. While this was unfortunate from the standpoint of overall model validation, the general characteristics of C. validus allowed flexibility with regard to this component. *Hyposoter fugitivus* (Say), a closely related species, was recovered from both ETC and FWW and hence studied in the field in the absence of *C. validus*. While much of *Hyposoter's* ecology will be dealt with in simulation, the following paragraphs will prove useful in terms of examining some factors contributing to parasite production. These factors will be discussed in terms of how *Hyposoter* interacts with each host independently. The interaction between all 3 of these populations will later be analyzed through use of the simulation model.

Immature parasite survival. Parasites which occur internal to their hosts are subjected to the same mortality factors as the host. This means that the parasite's distribution of mortality will follow very much the same patterns as the host. The probability of surviving to adult will therefore be dependent on the survivorship curve and time of attack, in addition to other phenomena such as egg and larval encapsulation, which add to mortality of the parasite alone.

Hyposoter adults prefer to attack early instars, and as such, are synchronized with early portions of ETC and FWW populations. For the tent caterpillar, *Hyposoter* adults emerge just prior to egg hatch and attack larvae issuing from egg masses before tent formation. In order for these adults to emerge earlier than ETC larvae they must overwinter in a stage which requires very little heat unit accumulation. The mode of overwintering is not known. Throughout this study adults occurred in the field as late as October when little or no host material was available. This suggests that *Hyposoter* may overwinter in the adult stage and have the ability to begin activity as soon as spring temperatures permit. Dunstan (1921) held adults of *H. pilosulus* in a cage under field conditions along with potential host material (*Ctenucha virginica* Charp.). Attacks on *Ctenucha* occurred late in the season and overwintering took place within the host larva. Along with this treatment, adults were held without host material, and a few individuals successfully overwintered as adults. It appears that *H. pilosulus* and presumably *H. f. fugitivus* may survive the winter in the adult stage providing that suitable hosts are unavailable. This is particularly important from the standpoint of attacking ETC larvae.

As mentioned, *Hyposoter* attacks the early instars, primarily the first through the third. In the ETC the first 3 instars occur in the field through 250 $D\text{-}D_9$. This means that successful attacks may occur throughout this period. However, if we take into account ETC's pattern of survival, then a slightly different picture emerges.

Because the survivorship curves in the ETC are nonlinear they provide *Hyposoter* certain periods of time which are optimal. Optimal, in the sense that there is a greater probability of producing adult parasites (P_A). This probability can be calculated by the following equation:

$$P_A = 1-(P_s(t)-P_s(t+dt)). \qquad [20]$$

Here, $P_s(t)$ is derived from equation 19 and is the probability of suriving to time t. $P_s(t+dt)$ is the probability of a larva surviving an additional dt degree-days. This dt represents the developmental time lag from deposition of a parasite egg until the host is killed.

The probabilities shown in Figure 16 apply to both the ETC and its parasites. However, they represent a mean condition for the tent caterpillar population and do not directly equate with parasite survival. Parasite eggs which are deposited in a host at any time t produce a probability of 1.0 that both host and parasite are there at that time. What this means is that a "sliding" scale must be used where P_A is 1.0 minus the difference between $P_s(t)$ (the time of deposition) and $P_x(t+dt)$ (the developmental time lag).

Hyposoter deposits eggs beneath the integument of ETC larvae and requires, under laboratory conditions, approximately 150 D-D_9 to kill its host. Further, susceptible life-stages of ETC occur in the field until about 250 D-D_9. Therefore, the time period of interest ranges from 0 to 250 D-D_9. Figure 19 presents P_A as a function of time of attack (t).

If one considers only the curves generated there are 2 periods of time when there will be a comparatively high probability for P_A (66% to 87%). The first period occurs within 100 D-D_9 of eclosion of tent caterpillar eggs. As might be expected, most Hyposoter oviposition occurred during this period. The second high probability region occurs between 225 and 250 D-D_9. During this time P_A was as high as 87%; however, this only considers ETC survival within the tent. Larvae which are attacked later than 200 D-D_9 will be in the dispersal phase. This means that estimates of tent related survivals will not apply. In fact, late stage

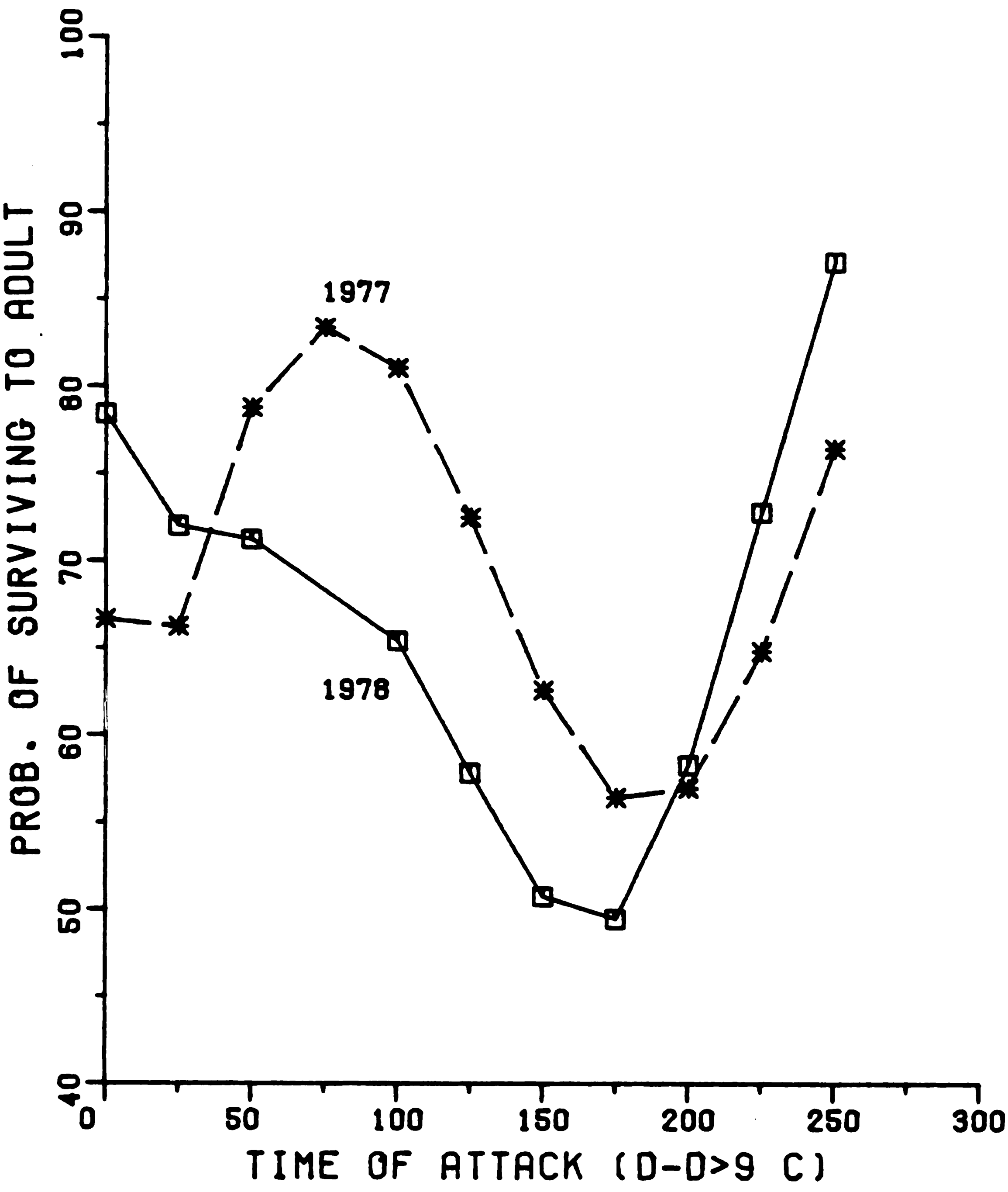


Figure 19. Probability of Hyposoter surviving to adult as a function of the time of attack on ETC.

survival away from the colony appears to be less than 10%, based on life table estimates (Table 2). Some individuals do not disperse from the colony and remain in the tent to pupate. Of those individuals, over 95% in 1977 through 1979 were parasitized by another parasite, *Itoplectis conquisitor* (Say). *Itoplectis* is able to out-compete or hyperparasitize *Hyposoter*, causing great amounts of mortality in both ETC and *Hyposoter*.

Assuming the host larva was not killed by other mortality factors, encapsulation of eggs or larvae is highly probable in instars 3-6. Morris' data (1976) shows encapsulation rates of 0, 36, and 74% for instars 1-3 in laboratory studies on the fall webworm. In a related species, *H. exiguae* (Viereck), 100% of eggs or larvae were encapsulated by host larvae which were third instar or older of *Peridroma saucia* (Hubner) (Puttler 1961). If these data are accepted as reasonable for ETC, then few *Hyposoter* eggs will produce adult parasites.

It should be noted that throughout this analysis we are under the assumption that survival of parasitized and nonparasitized larvae is the same. It may well be that behavioral changes in parasitized individuals avails them to greater or lesser amounts of mortality. Differential mortality of this sort has been demonstrated for the western tent caterpillar. Predators, parasites, and pathogens respond to the activity level of any particular WTC larva (Iwao and Wellington 1970a,b). Activity levels are a function of the individual and any factor such as parasitism which affects the individual. Hence, differences occur in an individual's survival value.

For *H. fugitivus* to attack the ETC, there is extreme selection pressure for attacks to occur within the first 125 D-D_9. This ensures that there will be at least a 50% probability of obtaining an adult parasite.

In terms of the FWW, the nature of the data collection (after a WMI of 3.5) does not allow calculation of P_A. We may, therefore, only speculate on Hyposoter's survival within the webworm colony and make comparisons with the ETC.

During the 3 years observed, Hyposoter parasitism in the FWW has been 50-95%. This is contrasted with the ETC where Hyposoter has attacked, at most, 25% of the larvae. There are many factors which may be responsible for the disparity in parasitism rates such as host density, parasite density, weather factors, and so on. However, possibly more significant than these are a series of parameters, most of which are intrinsic to either the ETC or FWW. In the analysis of Hyposoter survival in ETC it was observed that the length of time host larvae spent in larval stages was important in successful parasite attack. The time spent in susceptible life-stages was also an important factor. Other parameters which may be significant in producing parasites are colony size, number of generations (Hyposoter) attacking a particular host species, encapsulation rates, and the number of competing parasite species. Each of these variables is listed in Table 3 and their comparison provides the following results.

For tent forming insects the amount of time spent with the colony (= larval stages) affords the individual a certain amount of increased survival value. FWW larvae spent almost 3 times the amount of time in the larval stage as the ETC. Hence, the rate of mortality per D-D will be less in the webworm and allow more Hyposoter larvae to survive. In fact, when rates calculated from Morris and Fulton (1970a) are compared

Table 3. Comparison of ETC and FWW with reference to susceptibility to parasite attack.

	ETC	FWW
Time required for larval period (days at 21 C)	27.25	80
Time spent in susceptible stages (days at 21 C)	8.75	61.7
Mean colony size at 50% larval development	130	200
Number of potential *Hyposoter* generations	1	2
Encapsulation	0-10%	0-100%
Number of competing parasite species during study	3	5

with values for ETC found here, rates of larval decline are .60 and .47 larvae/colony/D-D for ETC and FWW, respectively.

The time spent in susceptible stages affords the parasite more or less opportunity to discover and parasitize hosts. Here, the FWW spends approximately 7 times longer in instars 1-3 than the ETC. Once again, higher probabilities of being parasitized are expected in the FWW.

Even though the size of a colony has no effect on the number of attacks in the colony, sheer numbers may provide a refugium for individuals. In other words, with increasing tent size the probability of being attacked decreases. By comparing the ETC and FWW, one finds that webworm colonies are 1.5 times as large as ETC colonies at 50% of their larval development. The 50% mark is used here due to sample program characteristics in the FWW. This allows us to utilize actual sample data from Gull Lake plots as opposed to extrapolations from the literature. All of the above comparisons directly apply to mortality rates in the hosts and indirectly to Hyposoter. In most cases the FWW has shown higher susceptibility to parasitism over the ETC and supports the parasitism rates found. Further support is given by the number of generations of Hyposoter which may potentially attack hosts with 2 in the webworm and 1 in the tent caterpillar. In opposition to these variables is encapsulation which commonly ranges from 50-100% in the FWW and less than 5% in the ETC. The number of observed encapsulations may, however, be related to the intensity of attack and thus comparison is not entirely justified. Also in opposition is the number of parasites competing for host resources and contesting Hyposoter. Three species were recovered from the ETC whereas 5 were frequently reared from the FWW. Multiple parasitism, however, was not a usual occurrence (< 3%).

Even though comparisons between tent caterpillars and webworms were done in a qualitative fashion, each piece of information lends support to the idea that the ETC moves through the system very rapidly and in this way avoids mortality factors. In contrast, the FWW is characterized by variability in emergence times, larval periods, and colony size, and in this way disperses mortality throughout the population. Hyposoter has also adapted to these strategies. In the spring, adults emerge before or simultaneously with ETC larvae and insure a maximum of successful attacks. Later in the summer Hyposoter produces 2 generations to encompass the entire length of time spent in susceptible life-stages by the FWW.

The interaction of ETC and FWW through their common parasites is the overriding theme of this research. A specific system was defined and analyzed in terms of its individual components and their direct interaction with related components. The following section will combine the available information in a comprehensive simulation model including all of the components discussed previously.

A MODEL OF PARASITISM AND POPULATION INTERACTION IN THE EASTERN TENT CATERPILLAR--FALL WEBWORM SYSTEM

The utility of phenology and survival studies lies in the researcher's ability to use the results in further analyses and applications. In an analytical mode, the temporal interaction of populations and their impact on each other is basic to ecological theory. In an applied mode, questions concerning when and how many can be answered for population sampling and management considerations. In this portion of the study on the ETC-FWW system I will address both the analytical and applied areas.

From an analytical perspective this study seeks to examine how populations interact with system and environmental parameters. For example, what role does temperature play in seasonal parasite production? How do density relationships function within the context of a multiple host-parasite system? What effect does host population heterogeneity have on parasite success and long-term relationships? These and other questions are central to an ecological understanding of the ETC-FWW system.

Currently, there is no economic justification for management of tent caterpillars, webworms, or related parasite populations. However, from a heuristic standpoint, the system design naturally leads to applications in agroecosystems of similar character. One of the reasons for choosing this system was because it is thought that the principles generated are amenable to extrapolation.

In order to deal with the above questions, two approaches can be taken. First, a series of field-oriented studies could conceivably examine short-term population processes. In turn, long-term questions can and have also been studied in the field. However, system noise, a posteriori realization of data gaps, time constraints and resource limitations reduce their effectiveness.

The second approach involves the use of computer simulation models. In this case, the only constraints imposed on analyses are lack of funds designated for such uses, computer size, creativity of the researcher and, of course, the data base. Depending upon the objectives of the modeling effort, possibly the key factor here is creativity. This implies that the researcher be specifically concerned with a set of sufficiently interesting queries regarding input/output relationships. Parameters which are not available empirically can be substituted with reasonable assumptions and designated as researchable for later study. The end result provides a set of "haves" and "have nots" as well as parameters and functional relations to be further explored. In the past, research has often ended with a modeling effort. Although these models have performed in each of the above capacities, they need to be used as an aid in mental processes at each stage of a project. The initial stages of research in particular require rigor and systems analysis utilizing simulation models to provide well defined structure to research in applied ecology.

Prediction is still another use of a simulation model. Numerous models have been put together with the objective of making predictive statements both quantitative and qualitative. Even though the end result may provide good probabilistic statements as to system response, their principal role in research still remains with the interesting questions posed and needed parameter studies.

The Aggregate System

The ETC-FWW system represents a system which is at best imperfectly known. A simulation model was developed at the outset of research and used to define and summarize the state of knowledge. The model was also and most importantly used in the development of concepts. Because of this, it is not necessary to mimic the real world system verbatim. For example, a priori model development dictates that all pest and parasite components be explicitly defined. For reasons stated earlier, the system includes the tent caterpillar, webworm, and *Campoplex validus*. It was shown that *C. validus* was not recovered during field studies. However, a related species, *Hyposoter fugitivus fugitivus*, was recovered. This would seem to immediately invalidate the model. On the other hand, C. validus was chosen because of its generalizeable characteristics. As such, statements concerning component and system response can still be made. In fact, a qualitative validation of the model under these circumstances demonstrates its ability to extrapolate to similar systems and the robustness of this technique.

I have stated in very general terms the intellectual pursuits of the model. In addition, a number of specific ecological questions have been asked. They are as follows:

1) How do system and environmental parameters affect time synchronies and rates of parasitism?
2) What is the system's response to various density relations within a growing season?
3) How do 1) and 2) affect long term system responses (multiseason)?
4) How does the system respond to management-oriented harvesting strategies?

The Eastern Tent Caterpillar

The ETC component is made up of a single series of time-varying distributed delays (TVDD) simulating a normal unparasitized flow of individuals. As mentioned earlier, each delay is characterized by DEL and k related to the mean and variance of the delay process (Eqs. 8, 9) ($k = 12$). DEL_i (days to develop) is determined at every point in time by instantaneous temperatures (T) generated from the sine wave technique and time-temperature functions derived experimentally. These functions take the form:

$$DEL_i = 1/A + BT \qquad [21]$$

where A and B are regression coefficients. This equation is used throughout the larval stages of the ETC model with Table 4 presenting the stage-specific coefficients. The functional form of the equation for tent caterpillar eggs is slightly different and is specifically:

$$DEL_E = T/-32.29 + 0.64T. \qquad [22]$$

Thus, an impulse type input is given to the series of egg and larval delays and individuals flow through stages at rates specified by equations 7, 21, 22, and temperature derivations. This model is portrayed in the functional block diagram in Figure 20 labeled NORMAL FLOW. For this component I have only included egg and larval stages, as pupal and adult dynamics are assumed to be insigificant insofar as parasitism is concerned.

Survival coefficients (Si) are treated in terms of mean values and are allowed to randomly vary ± 10%. Coefficients are applied at the end of each life-stage. These coefficients are listed in Table 4 and derived in an earlier section treating stage-specific survivals. As mentioned in that section, stages 5-A were combined for an aggregate survival rate (ca. 0.05). Because of this aggregation, S_5 and S_6 had to be estimated. This was done by dividing the 0.05 survival among the four life-stages equally. An alternative to this would be to weight survival coefficients as a function of the amount of time spent in the particular instar. This proved to be unsatisfactory in that a fifth instar survival of 0.67 appears to grossly overestimate the trend indicated by previous instars and survivorship curves presented earlier. Equal weighting produces a more satisfactory late stage survival.

The output produced from the normal flow includes the number of individuals in each life-stage and the maturity of the population at any point in time (WMI). Output from the sixth instar gives the exact number

Table 4. Eastern tent caterpillar delay parameters.

Life-stage	Degree-Day Requirements		Time-Temp. Parameters (°F)		Survival Coefficient
	$D\text{-}D_{48}$	$D\text{-}D_9$	A	B	
Egg	118.75	65.97	†-32.28929	0.63973	0.84
L I	63.00	35.00	-0.76377	0.01585	0.94
II	63.00	35.00	-0.76377	0.01585	0.90
III	63.05	35.03	-0.76377	0.01585	0.77
IV	82.33	45.74	-0.57937	0.01203	0.49
V	102.30	56.78	-0.47243	0.00980	0.47*
VI	214.88	119.38	-0.22435	0.00465	0.47*
Pupa	370.03	205.57	-0.13028	0.00270	0.47*
Adult	72.00	40.00	--	--	0.47*

*Individual coefficients are not available. Survival is distributed evently from V-A. Survival from V-A is 0.05

†See text for form of equation.

of larvae entering the pupal stage. This, along with pupal and adult survival and fecundity, can then be used to make predictions as to the overwintering egg population.

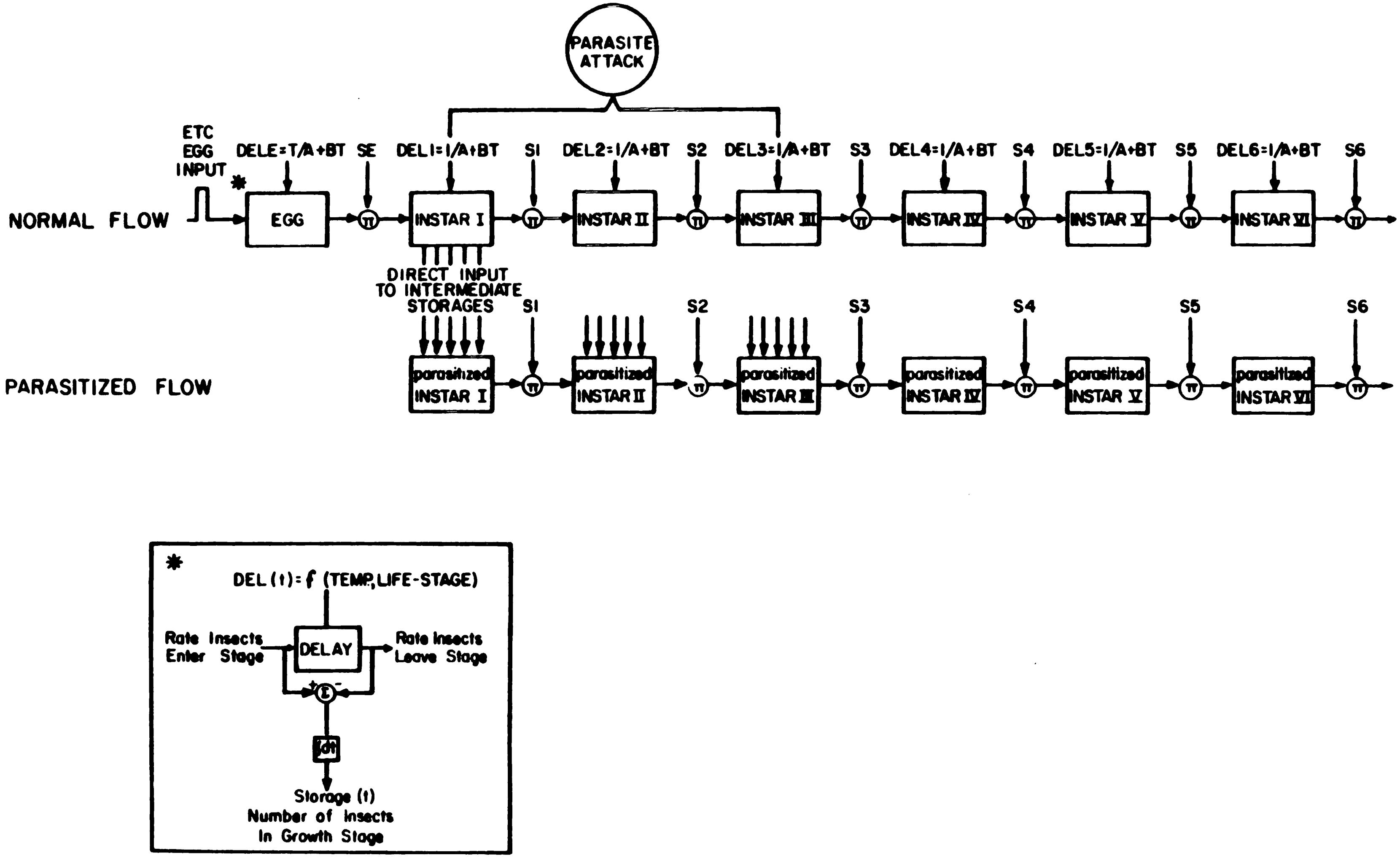
Campoplex Attack on the ETC

C. validus has been shown to attack only instars 1-3 in the webworm and it is assumed that the same preference occurs in the tent caterpillar. *Campoplex* deposits a single egg beneath the integument of these early stage larvae. Once parasitized these larvae are not reattacked. Thus, parasites are able to discriminate between parasitized and non-parasitized individuals. This aspect is handled explicitly in the model by removal of individuals from the normal ETC flow and using them as inputs to a parasitized flow (Fig. 20).

A unique aspect of the removal of parasitized individuals is that the within-instar age of an individual is retained after parasitism. In other words, a larva which has developed 80% through a given instar will be placed in exactly that same position in a parallel parasitized flow. Further, the fact that parasitized larvae are taken directly from within the delay insures that parasites respond only to non-parasitized densities. This technique is not without its faults. Laboratory studies have demonstrated that parasites will respond in some manner to larvae which have been parasitized. Even though the parasite may ultimately reject the host, a significant amount of searching time can be used in this activity. Thus, attack rates are reduced as a result of this type of interference (Griffiths and Holling 1969, Hassell and May 1974).

By the end of the third instar, no further parasitism takes place. Larvae move through parallel flows in identical fashion with the parasitized

Figure 20. Functional block diagram of ETC component. (Inset: Generalized time varying distributed delay (Manetsch 1976)).


PARASITE ATTACK
NORMAL FLOW
ETC EGG INPUT
*
DELE=T/A+BT
SE
DEL1=1/A+BT
S1
DEL2=1/A+BT
S2
DEL3=1/A+BT
S3
DEL4=1/A+BT
S4
DEL5=1/A+BT
S5
DEL6=1/A+BT
S6
EGG
INSTAR I
INSTAR II
INSTAR III
INSTAR IV
INSTAR V
INSTAR VI
π
DIRECT INPUT TO INTERMEDIATE STORAGES
PARASITIZED FLOW
parasitized INSTAR I
parasitized INSTAR II
parasitized INSTAR III
parasitized INSTAR IV
parasitized INSTAR V
parasitized INSTAR VI
*
DEL (t) = f (TEMP, LIFE-STAGE)
Rate Insects Enter Stage
DELAY
Rate Insects Leave Stage
+
-
Σ
∫dt
Storage (t)
Number of Insects
In Growth Stage

larvae producing the second generation of Campoplex to attack webworm larvae. Because of insufficient data it is assumed that parasitized and non-parasitized larvae behave similarly and have the same fitness. Therefore, survival coefficients apply equally to both flows.

The attack model. The attack function is a result of modifications made to the Holling (1959) "disc equation" and the Griffiths and Holling (1969) competition submodel. Attacks per parasite (A) are generated using:

$$A = \frac{aTH}{1 + a\,T_H\,H} \qquad [23]$$

where:

a = the instantaneous rate of discovery,

T = the time available for search,

T_H = the handling time, and

H = the host density.

Total attacks for the population are a linear function of the parasite density P or:

$$N_A = AP \qquad [24]$$

Use of equations 23 and 24 assumes a random search by parasites (i.e., each individual in the host population has an equal opportunity to be attacked). We may expand this idea to the case where attacks are distributed other than randomly. The equation:

$$N_G = H\left[1 - \left(1 + \frac{N_A}{Hk}\right)^{-k}\right] \qquad [25]$$

takes into account the fact that attacks may be distributed in a contagious fashion (Griffiths and Holling 1969). Here:

N_G = the gross number of attacks,

H = the host density, and

k = the negative binomial parameter, or in its simplified form:

$$k = \frac{\mu^2}{\sigma^2-\mu} \qquad [26]$$

for mean μ attacks and variance σ^2. The parameter k varies between zero (strong clumping) and infinity where the negative binomial becomes poisson. For this model (Eq. 25) the proportion of hosts attacked is one minus the probability of zero attacks, q, where q is given by:

$$a = 1 + \frac{N_A}{Hk} \qquad [27]$$

For Campoplex, k is set of 100 indicating a random distribution of attacks (Salt 1934). Strictly speaking, equation 25 can be reduced to a random distribution but is retained for flexibility.

For this type of model, where system dynamics are simulated on a within day basis, it is not reasonable to assume that parasites are always in an attack mode. This aspect is considered in two ways. First, the time available for attack is assumed to include only the daylight hours. Second, temperature affects are taken into account by reducing attacks during temperatures less than 65° F (18.33° C) and greater than 90° F (32.22° C). Attacks are reduced by a linear function with a slope of 0.1 at temperatures between 60° F (15.56° C) and 65° F (18.33° C). Between 90° F (32.22° C) and 110° F (43.33° C) the slope is 0.05. Figure 21 demonstrates this function along with effects of host density. This is essentially a graphical representation of the attack model.

Models for Development in C. validus

Simulation of life-stages in *C. validus* is accomplished using the delay techniques described earlier. A simulated growing season begins with an impulse type input into the pupal delay. Adults are produced from the output and used as inputs to the attack model. Immature stages of *Campoplex* flow through host larval stages in rates determined by the host. Upon reaching the end of the sixth instar (in ETC and FWW) output from this delay produces the second generation when attacking ETC, or the overwintering generation when attacking FWW. Table 5 gives the delay parameters used for adult and pupal stages of *Campoplex*. The time-temperature function is that of equation 21.

Table 5. *C. validus* delay parameters.

Life-Stage	$D\text{-}D_{42}$	$D\text{-}D_{5.5}$	Time-Temp. Parameters (°F) A	B	Survival Coefficient
Adult	625	347	-0.06719	0.00159	1.00
Pupa	175	97	-0.23993	0.00571	1.00

The Fall Webworm

Characteristic of FWW populations is a tremendous amount of variability in adult moth emergence. More specifically, a larger variance is associated with the heat requirements for diapause termination in overwintering pupae (Morris and Fulton 1970a). Correlated with this variability are certain fitness responses such as fecundity and larval survival. It appears that heat requirements are under genetic control and therefore, in part, responsible for the survival value of that particular phenotype. Morris (1971, 1976) and Morris and Fulton (1970a,b) have examined these relationships and produced a series of regression models to describe the relationship between requirements for adult moth emergence and survival. These models, along with the developmental delays, form the basis for the FWW component.

The genetically controlled emergence of the webworm dictates that different portions of the population will be subjected to different types of mortalities (e.g., changing food quality). In addition, differential overwintering success and larval ability to encapsulate parasite eggs are correlated with the genetics of the individual. Because of the extreme differences in individuals, survival becomes a dynamic entity and must be explicitly modeled in the FWW component.

Simulation of Mating, Development and Survival in the FWW

Within the model the degree-day requirements for adult moth emergence (i.e., the pupal delay) are divided into ten discrete blocks or phenotypic classes symbolized as "Kp classes" ranging from 280-720 D-D_{11} in 40 D-D_{11} increments. Each of the Kp classes is simulated separately, producing a total of ten flows for the unparasitized webworm component (Fig. 22). Independent simulation of the ten classes enabled the assignment of coefficients to govern encapsulation, survival, and developmental rates (Table 6). Each Kp class is then represented by a series of TVDD's simulating all life-stages of the FWW.

As with the ETC and *Campoplex*, instantaneous values for the delays are calculated from laboratory data generated in this study and information from Morris and Fulton (1970a).

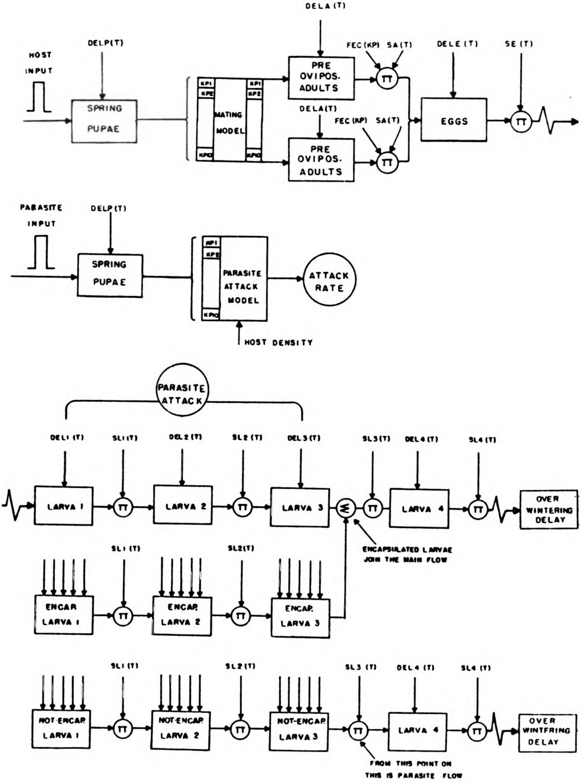


Figure 22. Functional block diagram for the FWW component. One of 10 flows is represented.

Table 6. Fall webworm pupal delay parameters.

	Degree-Day Requirements		Time-Temp. Parameters			
K_p	$D\text{-}D_{51}$	$D\text{-}D_{11}$	A	B	Survival Coefficient	Pupal Weight
1	320	178	-0.15944	0.00313	0.40	150
2	360	200	-0.14178	0.00278	0.40	153
3	400	222	-0.12755	0.00250	0.40	155
4	440	244	-0.11593	0.00227	0.40	155
5	480	267	-0.10624	0.00208	0.40	154
6	520	289	-0.09810	0.00192	0.40	153
7	560	311	-0.09107	0.00179	0.40	150
8	600	333	-0.08499	0.00167	0.40	144
9	640	356	-0.07969	0.00156	0.40	139
10	680	378	-0.07499	0.00147	0.40	128

Survivorship or the transfer coefficients for each life-stage (i.e., S_E, S_1, S_2 ...) are applied at the end of each stage. These coefficients, like those of the ETC, were determined through life-table studies and allowed to randomly vary ± 10%. Because of the endemic level of webworms throughout this study, coefficients were taken from Morris (1967, 1972) and Ito and Miyashita (1968). Coefficients for development and survival are listed in Table 7.

Simulation of the webworm component begins by providing impulse inputs to the pupal stage of each of the Kp classes (Fig. 22). Webworms are held within the pupal delays as specified in Table 6. Upon adult emergence, mating begins and is completed by the third day after eclosion (Morris and Fulton 1970a). As the mating period for an individual is short (1-3 days) and the total emergence time is quite long, mating is positively assortive with respect to Kp. That is, early individuals (low Kp) mate with early individuals and late (high Kp) with late.

Because the output from pupal delays is time distributed, there is some overlap in emergence. This, together with the fact that some individuals may wait as long as 3 days to mate, ensures that there will be gene flow throughout the population. Within the mating model, 65% of the moths mate the day of eclosion (A). The remaining 35% enter one of two discreet delays, the first of which holds 23% of the moths for one day (B). The second holds 12% for a two-day delay (C) before mating (Fig. 23). Kp values for mating moths are calculated from the cumulative degree-days (CUMDD(t)) and the length of stay in the premating delay. Moths in mating class A have a Kp value equal to CUMDD(t), while B and C have Kp values of CUMDD(t) minus the degree-day accumulation while in their respective mating delays. Since three types of mating individuals

Table 7. Fall webworm delay parameters (excl. pupae)

Life-stage	Degree-Day Requirements $D\text{-}D_{51}$	$D\text{-}D_{11}$	Time-Temp. Parameters A	B	Survival Coefficient
Egg	240	133	-0.21237	0.00416	0.85
L I	114	63	-0.44778	0.00878	0.55
II	91	51	-0.55997	0.01098	0.75
III	91	51	-0.55997	0.01098	0.70
IV	114	63	-0.44893	0.00880	0.60
V	166	92	-0.30672	0.00601	0.45
VI	223	124	-0.22863	0.00448	0.45
Adult	150	83	-0.34018	0.00667	0.75

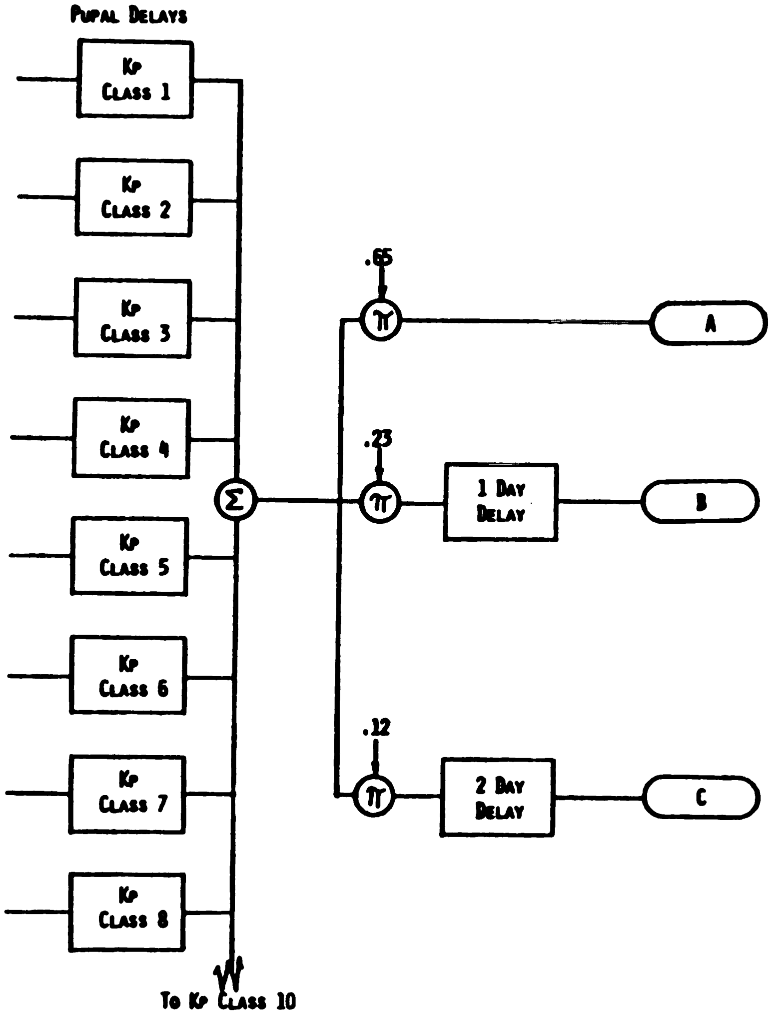
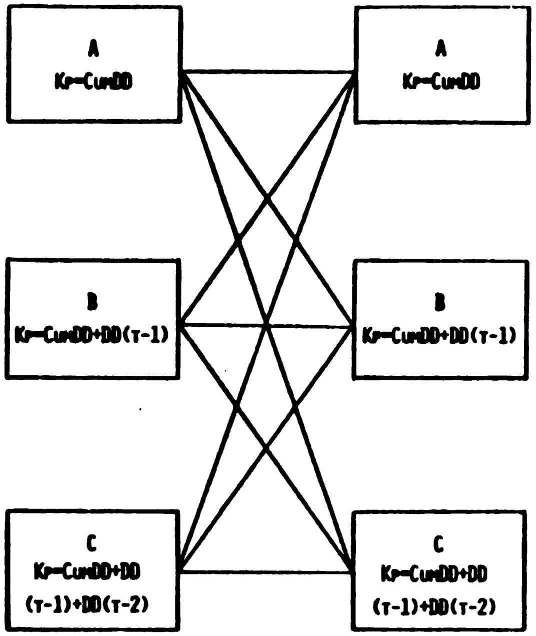


Figure 23. Discrete mating delays.



Mid-Parental Kp Calculations ($\bar{\text{K}}$pp)

AA=CumDD

BB=CumDD+DD(τ-1)

CC=CumDD+DD(τ-1)+DD(τ-2)

AB=(2•CumDD+DD(τ-1))/2

AC=(2•CumDD+DD(τ-1)+DD(τ-2))/2

BC=(2•CumDD+2•DD(τ-1)+DD(τ-2))/2

Figure 24. Mating model.

are found at any time, the possible cross-matings are: AA, AB, AC, BB, BC, and CC. Figure 24 shows these cross-matings along with equations for calculating individual Kp and mid-parental Kp for each mating combination. Through this type of recombination evolves the population heterogeneity in terms of development and survival throughout the range of Kp classes.

The mid-parental Kp ($\bar{K}pp$) is used directly in determining the distribution of Kp for the resulting offspring (colony). The mean Kp for the colony ($\bar{K}pc$) is calculated by the regression equation:

$$\bar{K}pc = e^{(2.456 + \bar{K}pp^{0.602})} \qquad [28]$$

(Morris and Fulton 1970b). The resulting $\bar{K}pc$ is then used in determining the within colony variance and standard deviation (SD) where:

$$SD = -1328.82 + \bar{K}pc^{229.665}. \qquad [29]$$

Within a colony it is assumed that Kp's are normally distributed. Means obtained from equation 28 are normalized, distributed about the normal curve, and once again divided into the ten discreet Kp classes. The number of eggs/colony are determined from $\bar{K}pp$ where:

$$\text{Eggs} = -134.0 + 3.8 \text{ (pupal wt)}. \qquad [30]$$

$\bar{K}pp$ is used here in its relationship with pupal weight. Pupal weight is determined for each Kp class derived under laboratory conditions (Morris and Fulton 1970b). Table 6 gives these values.

Campoplex Attack on the FWW

Parasite attack on the FWW is simulated as described in the ETC. Significant differences, however, lie in two areas. First, the 10 Kp classes each have parallel flows for parasitized larvae. Second, once in a parasitized flow, attrition may occur due to reductions proportional to larval survival coefficients and encapsulation of Campoplex eggs. Encapsulation is modeled similar to parasite attack in the unparasitized flows. Individuals are removed as a function of instar and Kp class and serve as inputs to encapsulated flows (Fig. 22, Table 8). Because of the perfect discrimination of parasitized larvae (encapsulated and not encapsulated) by Campoplex, 30 flows must be individually simulated. Host larvae are only parasitized once. At the end of the third instar, the encapsulated flows join the unparasitized flows due to the fact that parasite attack is not involved after the third instar. Thus, there is no reason to continue to "track" larvae with encapsulated parasite eggs. The parasitized flows continue until the sixth instar, during which death of the host larva occurs and parasite pupae are generated.

Listing of the entire simulation model is given in Appendix A.

Model Validation

Validation of a simulation model demonstrates the degree of realism embodied in the model. Comparisons can be made utilizing field observations of both quantitative and qualitative nature concerning various aspects of model structure and response to stimuli. For the ETC-FWW simulation, outputs are verified with field observations made at Gull Lake, Michigan, in 1977 through 1979. Comparisons will be made with reference to each modeled population for the following aspects:

1) temporal occurrence,
2) larval population maturity,
3) patterns of survival,
4) trends in yearly population build-up or decline, and
5) trends in rates of parasitism.

Table 8. Fall webworm encapsulation coefficients.

Kp class	1	2	3	4	5	6	7	8	9	10	Stage-Specific Coefficient
Kp Specific Coefficient	0.60	0.52	0.42	0.37	0.29	0.22	0.15	0.08	0.0	0.0	--
Instar:											
LI	0.60	0.52	0.42	0.37	0.29	0.22	0.15	0.08	0.0	0.0	1.0
II	0.90	0.78	0.63	0.56	0.44	0.33	0.23	0.12	0.0	0.0	1.5
III	1.00	0.86	0.70	0.61	0.48	0.37	0.25	0.20	0.0	0.0	1.66

Eastern tent caterpillar validation. In an earlier section, laboratory hatch rates were compared with field observations and were highly correlated. Field observations were taken, however, on a per mass basis, whereas laboratory measurements could be taken for a population of individuals. Because the field and laboratory populations compared favorably and because laboratory estimates were done on a per individual basis, I will examine the simulation results of egg hatch with reference to lab results. This method is not entirely valid because delay values for the egg stage were derived from a summary of this laboratory data. This means that our validation contains some elements used in determining DEL and K values for the time-varying distributed delays. We do know, however, that the 1, 50, and 100% cumulative hatch points on the curve do have validity under field conditions (see "Phenology Models in the Eastern Tent Caterpillar").

Figure 25 presents the simulated and observed egg hatch data. It is apparent that the two curves are quite similar but differ in temporal placement.

During the ETC hatch period degree-day accumulations average approximately 3 $D\text{-}D_9$/day (1976-1979). In terms of percent hatch, this means that the actual hatch may be overestimated by as much as 25%, were the original values to be used. In order to determine the degree to which the model and field observations differ, observed values were regressed on model estimates of percent hatch. If the values are identical, then we expect to obtain a y-intercept of 0.0 and a slope of 1.0. Results of the analysis produced the equation:

$$\text{Obs} = -12.86 + 0.9729 \text{ Mod} \qquad [31]$$

$$r^2 = .8439$$

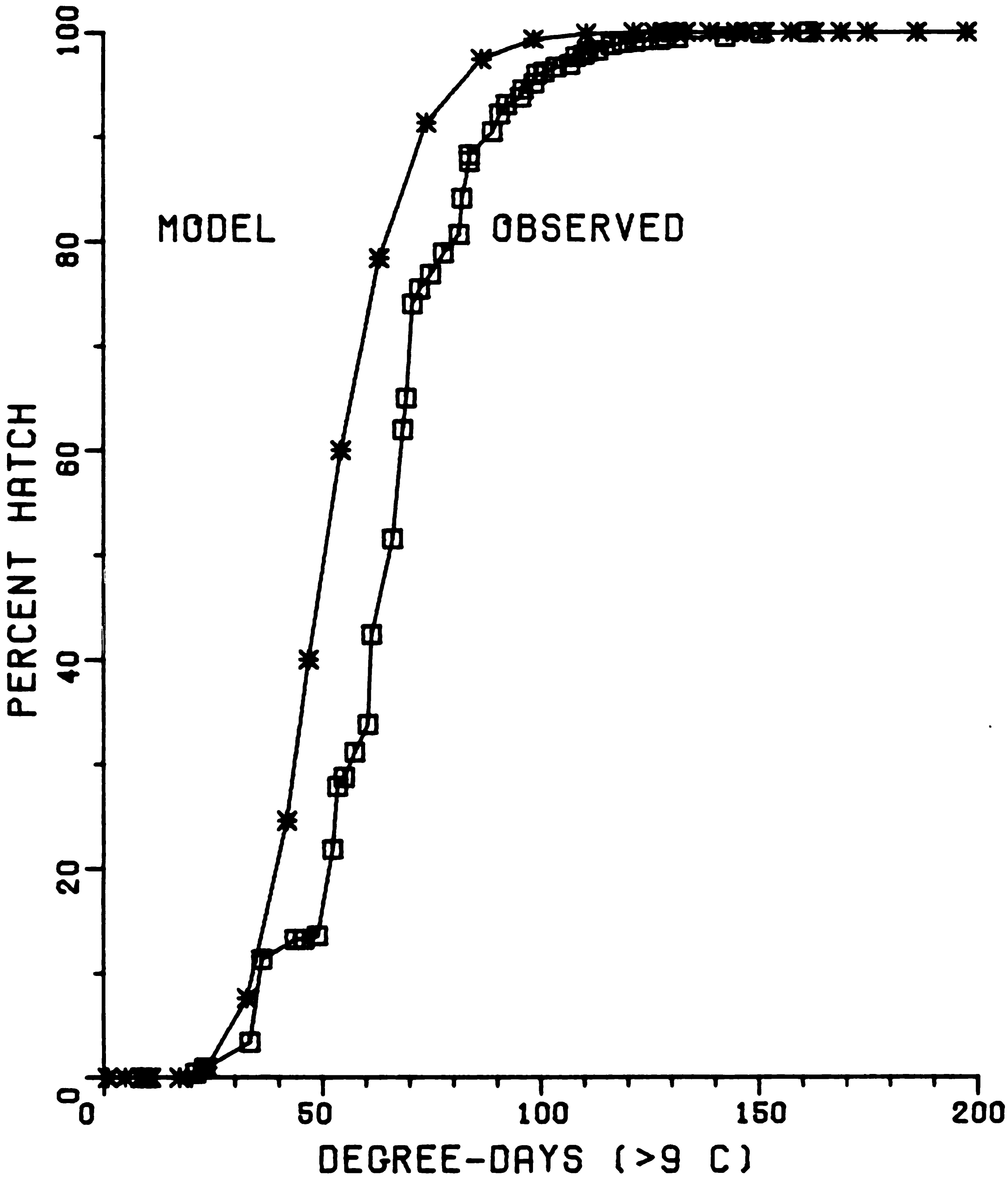


Figure 25. Comparison of observed and predicted ETC egg hatch rates.

Without resorting to tests of significance, a slope of .97 is reasonably close to 1.0 and indicates that the rate of egg development is not different from observed values. The intercept of -12.86 indicates the number of degree-days that the curves are shifted. Thus, 12.86 D-D_9, or its equivalent in chronological time, is added to the time-temperature function for egg development.

Another model output which can be compared with field results is the maturity of the larval population through the growing season. In order to examine this, a weighted mean instar was calculated (Eq. 13) from population samples taken at Gull Lake and compared with simulation results (Figs. 26, 27). These estimates are not significantly different ($p < .05$) with model results providing a good prediction of larval population maturity for 1977 and 1978.

Based on the results of ETC egg hatch and larval population maturity, the simulation model behaves well phenologically. Rates of development do not differ significantly from observed values and temporal occurrence of the immature life-stages agree with the natural population.

The pattern of mortality in simulated and observed populations provides an additional piece of validation data. Results of this comparison are shown in Figure 28. What the model actually presents is the distribution of mortality within the colony for nondispersive larval stages and survival associated with dispersal from 200 D-D_9 on. Because of this, it would be expected that the model may provide good survival estimates of the whole population, but differ from the larval population examined in tent sampling. For the most part, the model agrees with observed values for 1978 but deviates early in the year (< 175 D-D_9) by about 10%. This discrepancy may be explained by the allowance of the

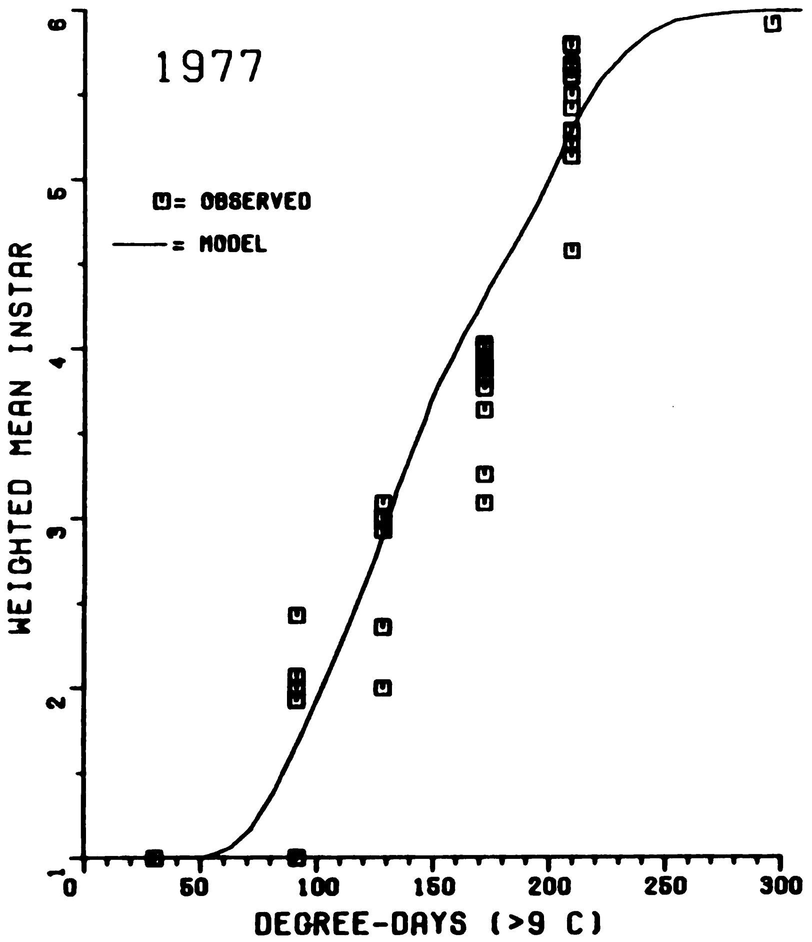


Figure 26. Comparison of observed and predicted ETC weighted mean instar for 1977.

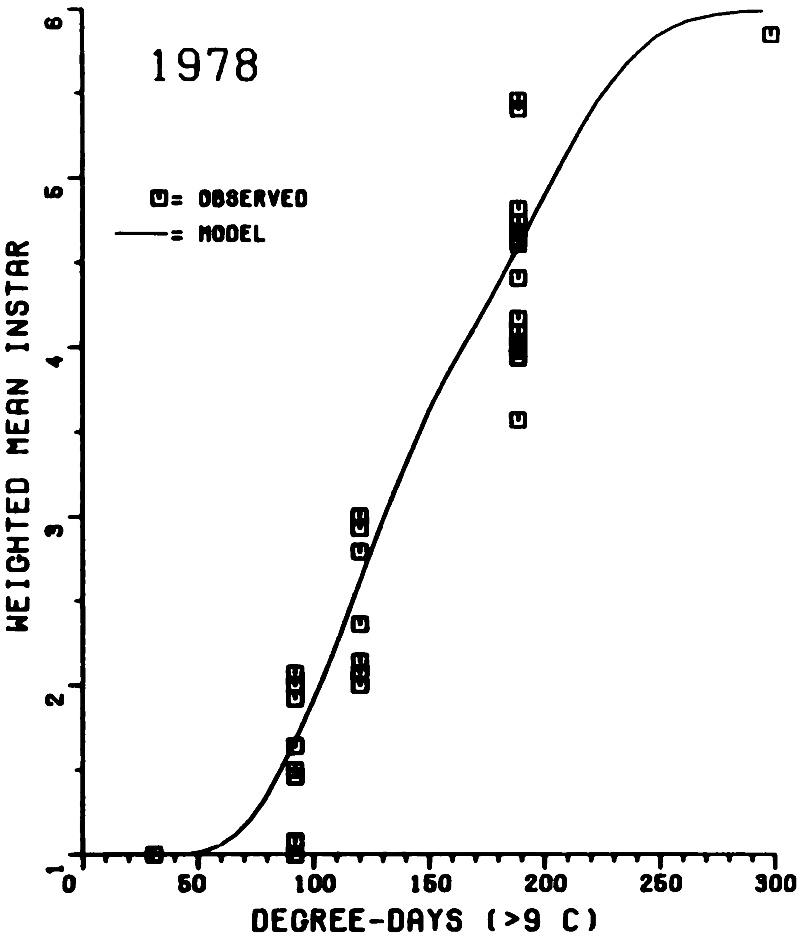


Figure 27. Comparison of observed and predicted ETC weighted mean instar for 1978.

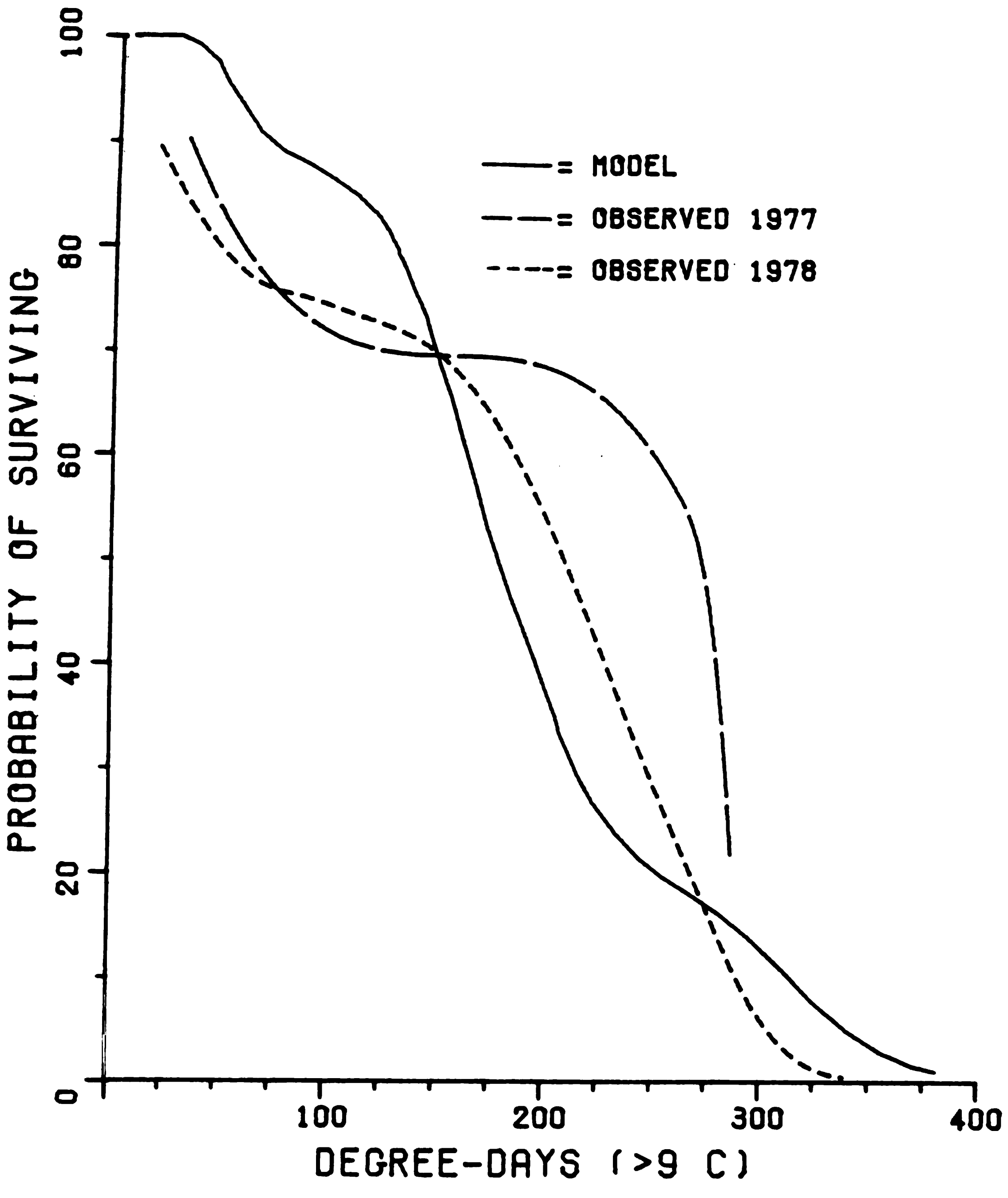


Figure 28. Comparison of observed and predicted ETC survivorship curves.

model to randomly fluctuate ± 10% about the mean values. Also, by applying survivals at the end of life-stages rather than continuously, there is a tendency to overestimate populations. Thus, the period from 0 to 175 D-D_9 overestimates due to random variability and the method used in application of mortality. The 1977 curve has a somewhat different form and plateaus from 150 to 250 D-D_9. It is not known why the survivorship curve assumes this form, although factors such as precipitation may play a role in larval dispersal. Colonies often remain intact longer during periods of precipitation and hence provide a different form to survival and dispersal.

It should be noted that Figure 28 indicates that tent caterpillars remain in the larval stage from approximately 20 to 400 D-D_9 and that this is the same range observed under field conditions for 1977 and 1978.

The technique of using laboratory-derived developmental information and time-varying distributed delays provides reliable estimates of phenological events. Adequate predictions of time of hatch, rate of hatch, time and rate of larval development, and seasonal population decay were produced from simulation results. It is felt that a realistic picture of ETC phenology has been produced from the model and may be used in the field or in future simulation experiments. Additional parameters such as parasitism and rates of population increase or decline will be examined with reference to the system as a whole in a later section.

Fall webworm validation. Validation of the webworm component of the simulation model presents problems which were not seen in the ETC. First, because Michigan populations were at low levels throughout the study period, data were not accumulated to the extent that they were in the ETC. Second, the webworm component was designed around populations studied by R. F. Morris in New Brunswick, Ontario. Morris' populations emerged as adults between 280 and 720 $D\text{-}D_{11}$ whereas Gull Lake webworms emerged between 600 and 1100 $D\text{-}D_{11}$.

Based on Morris' studies and the analysis of species concepts provided in Appendix F, it is expected that this type of shift could occur in emergence patterns. Developmental rates for larval stages appear to remain unchanged when moving south in the FWW's distribution. However, degree-day requirements for adult moth emergence (Kp) do vary. If this idea is accepted, then shifting the Canadian population by the appropriate number of degree-days should enable predictions to be made concerning any other webworm population. Shifting the median of the New Brunswick population by 420 $D\text{-}D_{11}$ produces estimates of larval incidence and weighted mean instar which are not significantly different from the Gull Lake population ($p < .05$).

Temporal placement of the FWW population and maturation rates are examined in Figures 29 and 30. If observed values are regressed on model estimates after taking into account the 420 $D\text{-}D_{11}$ difference, we obtain:

$$\text{Obs} = -0.1854 + 1.047\ \text{Mod} \qquad [32]$$

$$r^2 = .9691$$

The regression indicates that the intercept and slope are not different from 0 and 1, respectively. Thus, the hypothesis of changes in Kp relative to geography and climate appears justified and is validated for the two years examined.

In terms of larval survival, the model may be partially validated because of low level populations and characteristics of larval sampling. Figure 31 presents model estimates along with curves for 1977 and 1978 Gull Lake populations. Clearly, values obtained in simulation underestimate

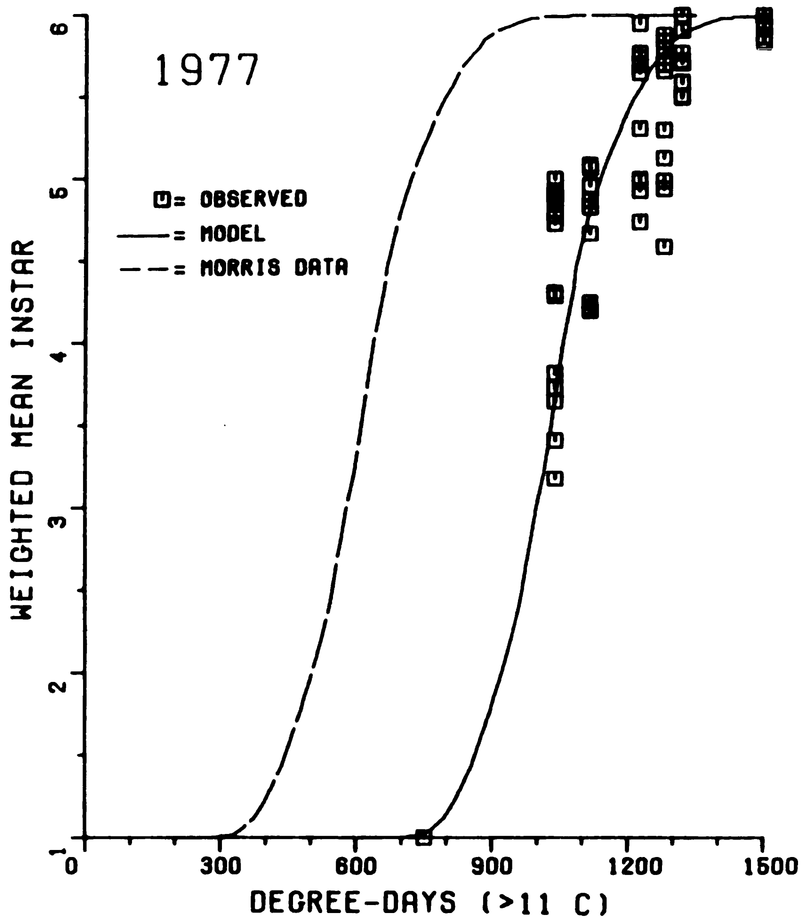


Figure 29. Comparison of observed and predicted FWW weighted mean instar for 1977.

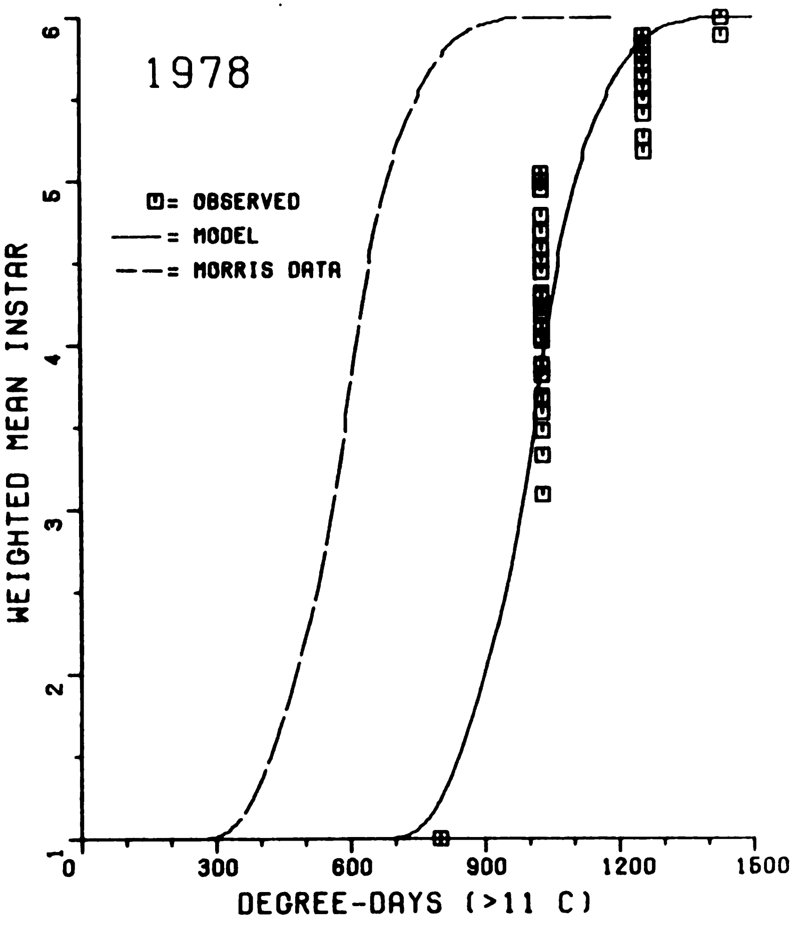


Figure 30. Comparison of observed and predicted FWW weighted mean instar for 1978.

survivorship from 1000 to 1500 D-D_{11}. The three curves are compared by the regression technique used earlier (Table 9).

Table 9. Comparison of model and observed survivorship curves for FWW.

	Model	1977	1978
Intercept	361.29	210.8	382.3
Slope	-.2558	-.1150	-.2558
r^2	.8631	.7601	.9219

For 1978, the model compares favorably with the rate of decline having idential slopes of -.2558, the differences occurring in the intercepts of the regression. On the other hand, 1977 values differ significantly from the model. It is not readily apparent why the slope is less than half that of 1978 values or the model estimates. Changes in foliage quality and timing of fall leaf drop may, however, affect the rate of decay. These factors are not taken into account in the model.

Because such differences in the magnitude and rates of mortality may occur from year-to-year and between locations, the coefficients used in simulation (Table 7) are retained as reasonable estimates with the decay rate corresponding well with 1978 data.

Population growth and parasitism. Criteria for this portion of the validation include rates of growth for each population and characteristics of parasitism. Two methods were used in validation: 1) the model was initialized with field data for 1977 and allowed to run through 1979; and 2) the model was initialized at the beginning of each year with field

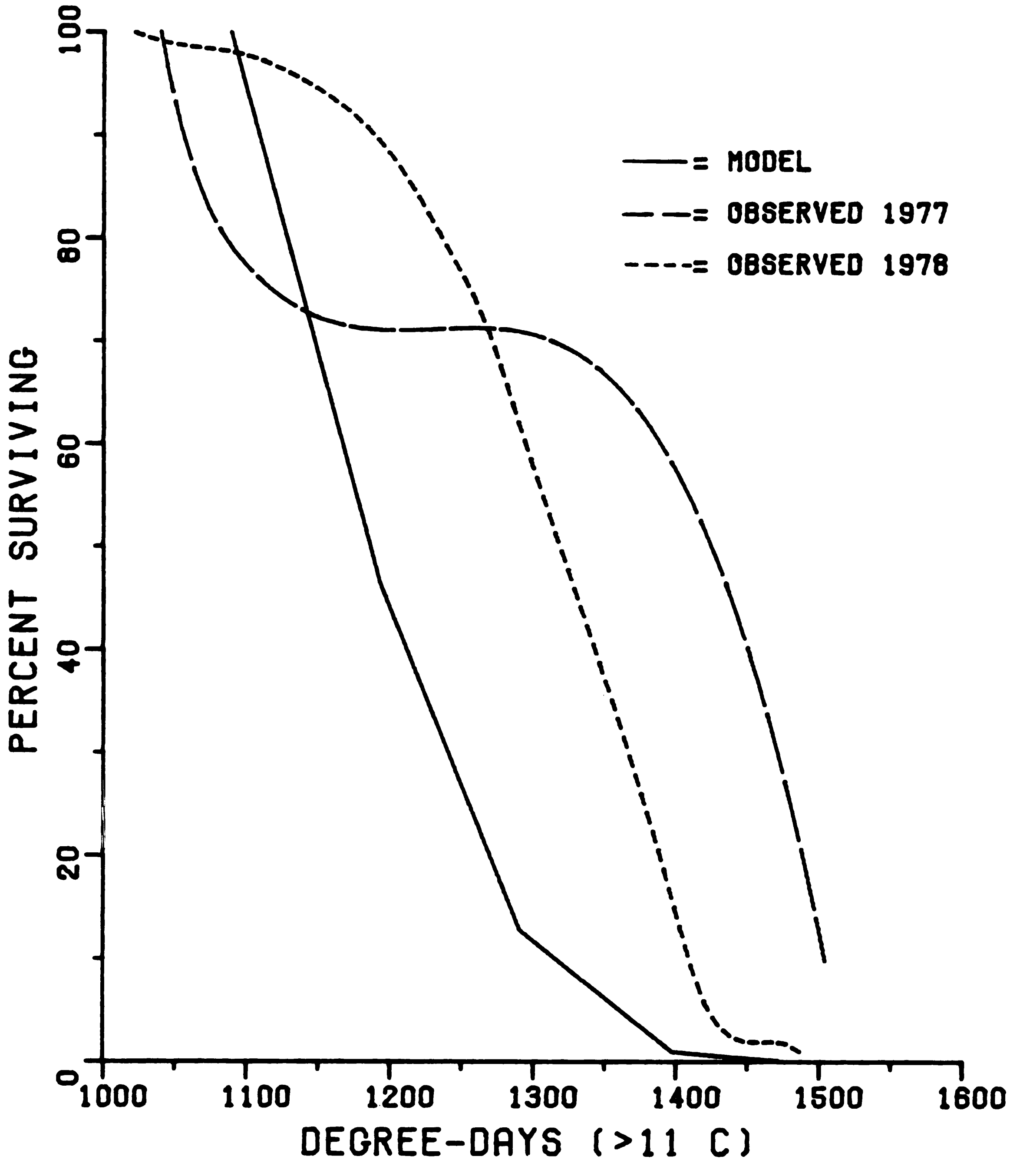


Figure 31. Comparison of observed and predicted FWW survivorship curves.

derived estimates. The results of these simulations were compared to field data for a 90 Ha. Gull Lake plot from 1977 through 1979.

For the first series of runs, the model was initialized with 1977 data and comparisons made of population statistics as listed in Table 10. In general, the output from 1977 overestimates each statistic for the tent caterpillar. Overwintering eggs are 24.07% greater, the number of colonies produced for the succeeding year are 4.28% greater, and the generation index, N(t)/Nt-1), is 0.08 larger than the observed value. This is not unacceptable in that the prediction of colonies for the 1978 season overestimated the true number by only 34 tents. This could conceivably be accounted for by the conservative estimate of egg mass size used (220 eggs/mass) or by any errors in population counts.

In terms of Campoplex, it is not possible to assess spring or initializing densities. As mentioned earlier, Campoplex was not detected within the field plots at Gull Lake. Hence, qualitative statements concerning the performance of the related species, H. f. fugitivus can only be made. It should be emphasized that this model represents the first iteration of a continuous process of reformulating concepts of system composition and parameterization. Further study would seek to build on the insight gained here. For 1977, the input to simulation was 10 parasites. This value was chosen based on preliminary runs and on the observed parasitism rate for that year. Even with this seemingly low density of parasites (0.11/Ha.) 7.94% of the simulated ETC population was parasitized as compared with 0.71% in the field situation. Clearly, a number of factors account for the discrepancy, the most obvious of which are species differences between Campoplex and Hyposoter. Under laboratory conditions, Campoplex may deposit as many as 22 eggs/day while Hyposoter

Table 10. Comparison of model and field results with the model, reinitialized with the previous year's output.

	1977		1977 w/Revised Attack		1978		1979	
	Observed	Model	Observed	Model	Observed	Model	Observed	Model
ETC eggs input	97000	97020	97020	97020	174900	217000	214500	512000
ETC eggs to over-winter	174900	217000	174900	221000	214500	512000	--	1210000
% parasitism	.71	7.94	.71	6.15	.41	2.87	8.29	1.65
Parasites produced	162.25	772	164.36	598	215	605	14937	8.38
Colonies (T+1)	795	829	795	844	975	1955	--	4620
Generation index	1.80	1.88	1.80	1.91	1.23	2.36	--	2.36
FWW pupal input	342	342	342	342	168	469	48	780
% parasitism	13.48	66.18	13.48	65.46	39.43	61.68	28.57	58.98
Parasites produced	8375.56	916.20	8375.56	905.70	5759	1254.80	1214.23	2111.80
Colonies (T+1)	60	94	60	96	17	156	--	294
Generation index	.35	.55	.35	.56	.28	1.66	--	1.88

may lay 3 (Morris 1976). If the attack function is altered proportional to the difference in eggs laid, this aspect can be examined. Even with the reduction in attacks, parasitism was only decreased by 1.79% and this does not account for differences with field data (Table 10).

Parasite-host synchrony could also account for differences in attack rates. Figure 32 shows the temporal coincidence of susceptible host stages and parasite populations as simulated. The ETC and Campoplex are well synchronized in this example for each year examined. Because of Campoplex's longevity, the entire susceptible host population experiences some level of parasite pressure. Under field conditions, Hyposoter attacks ended at 192 D-D_9, 134 D-D_9, and 139 D-D_9 for 1977 through 1979, respectively. Field data suggest that attacks end somewhat earlier for Hyposoter and that the later portions of the host incidence curve ($>$ 140 D-D_9) experience considerably less parasitism than simulated, particularly so in 1978. Attacks are also reduced in simulation with 1978 showing the largest decline in adult Campoplex incidence, and 1977 showing the least decline, beginning approximately 125 D-D_9 (Fig. 32). Statistical significance cannot be detected between the 3 years, but the trend in simulation and field estimates is similar, possibly due to differences in yearly temperature regimes.

Reinitializing the model with the previously simulated year's outputs produces instability in the model. By the end of 1977, 916 parasites were produced to overwinter. If this number is used along with ETC and FWW outputs, the tent caterpillar quickly goes to extinction by the end of 1978. Reinitializing in this manner implicitly assumes that 100% of the parasites will survive and remain within the area for the following spring. Under field conditions over 8000 parasites (Hyposoter) were produced by

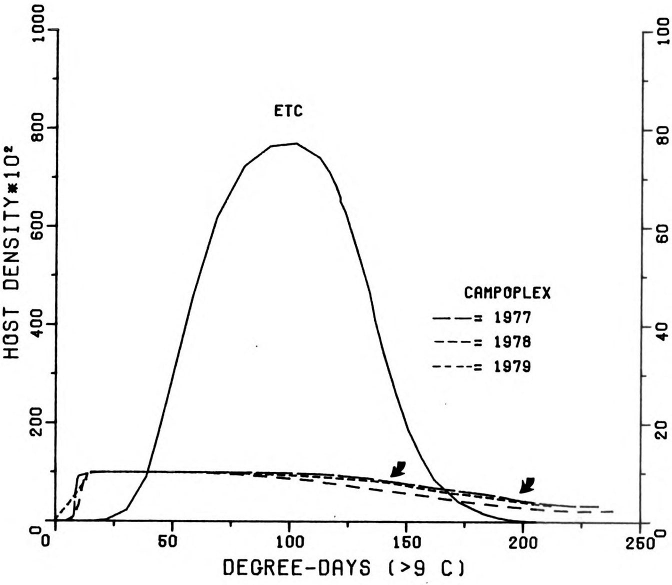


Figure 32. ETC larval and Campoplex adult incidence curves.

the end of 1977 and only 0.41% parasitism resulting in 215 parasites from the ETC at Gull Lake in the spring of 1978. In contrast, 5759 parasites overwintered at Gull Lake in 1978 and 14,937 were produced from the ETC in 1979 (Table 10). Thus, the relationship of overwintering parasites such as Hyposoter and Campoplex and those emerging in the spring is not clear. Further field studies are required to determine if the variation in spring densities is due to immigration or emmigration, or if hosts other than the FWW are being attacked later in the season. A number of other hosts are parasitized by both Campoplex and Hyposoter and may add to the overwintering generation. Low webworm densities can also serve to cause parasite dispersal away from areas and further reduce spring densities on a local basis. In either case, these factors are not considered in the model.

If the parasite density in the spring is held constant and the webworm and tent caterpillar are reinitialized with previous outputs, the generation index for ETC remains at 2.36 for 1978 and 1979. Under field conditions, the generation index for 1978 was 1.23. Thus, the rate of increase in the ETC is 1.9 times greater in simulation (Table 10).

An alternative to allowing the model to run continuously from year to year is initializing it each spring with known densities. This takes into account problems of estimating overwintering survivals and dispersal. Results of this provide a better estimate of ETC increase for 1978. Once again the observed generation index for 1978 was 1.23 with a revised model estimate of 1.88 (Table 11).

For the FWW, continuous model runs also lead to unacceptable results. As seen in Table 10, each successive year produces increasing numbers of webworms while actual field estimates indicate a decline in webworm

Table 11. Comparison of model and field results with model reinitialized with actual field counts.

	1977		1978		1979	
	Observed	Model	Observed	Model	Observed	Model
ETC egg input	97020	97020	174900	174900	214500	214500
ETC eggs to over-winter	174900	217000	214500	410000	--	496000
% parasitism	.71	7.94	.41	3.42	8.29	3.74
Parasites produced	162.25	172	164.36	598	14937	796
Colonies (T+1)	795	829	975	1565.45	--	1893.82
Generation index	1.80	1.88	1.23	1.88	--	1.21
FWW pupal input	342	342	168	168	48	48
% parasitism	13.48	66.18	39.43	65.80	28.57	65.20
Parasites produced	8375.56	916.20	5759	456.5	1214	129.82
Colonies (N+1)	60	94	17	47	--	13.85
Generation index	.35	.55	.28	.79	--	.29

density. Initialization of each year's run with known densities provides more acceptable results with overestimation of the number of colonies for 90 Ha.'s of 34 and 30 for 1978 and 1979. Further, the rate of decrease in population numbers prediced is similar to observed values (-43 and -47, respectively) (Table 10).

Parasitism and encapsulation in the fall webworm. Rates of parasitism in the webworm remained remarkably constant during simulation even though parasite production from the ETC ranged from 172 to 796. This is due, in part, to the impact of encapsulation on parasitism. As described earlier, encapsulation varies with instar and with the time of adult emergence (Table 8). This factor was examined using data collected from the Gull Lake study. Colonies were selected on the basis of having at least one attack in the larvae dissected from a colony. In addition to ascertaining whether an individual had been parasitized and the egg of *Hyposoter* encapsulated, the number of eggs laid, the position of the egg in the host, and the age of the host were also determined. A forward step-wise multiple regression was performed with percent encapsulation (PCTE) regressed on the above factors. To take into account the aspect of time of adult emergence (Kp) and encapsulation, it was assumed that, at the colony level, if a group of larvae had emerged earlier than another, then the average age of those individuals would be greater. This age factor was measured in terms of a weighted mean instar (Eq. 13).

Results of the regression showed that position in the host and number of eggs laid were significant in determining encapsulation levels ($p < .05$). Age of the individual, on the other hand, was not significant (Table 12). The fact that the time of emergence (Kp) and encapsulation were not significantly correlated does not necessarily invalidate assumptions made in the model. That is, calculating Kp in the manner described will add significant amounts of variability to the relationship. For example, each colony examined was subjected to different temperatures, food qualities, and other factors considered a part of the microclimate. Each of these factors contributes to the variance associated with colony maturity along with the time of emergence.

Table 12. Regression statistics for _Hyposoter_ egg encapsulation.

Variable	F to Enter or Remove	Significance	r^2	Overall F	Significance
Position (POS)	7.25**	0.01	0.13	7.25	0.010
No./Host (N/H)	4.41*	0.04	0.20	6.08	0.004
Wtd. Mean Ins.	0.42 n.s.	0.52	0.21	4.14	0.011

$$PCTE = 28.99 + 55.06 \ln POS + 48.49 \ln N/H$$

* (p   .05)
** (p   .01)

In terms of position, two factors are significant. First, 89.59% of all _Hyposoter_ eggs laid were deposited posterior to the fourth set of prolegs. Of the remaining ovipositions, 8.78% were placed in the area of the prolegs and 1.63% were anterior to that. Second, given that an egg had been laid, there was a 0.1868 probability of being encapsulated in the posterior section, 0.3953 in the mid-section, and 0.50 for the anterior portion. Combining these numbers produces the probability of oviposition _and_ encapsulation for each section; 0.1679, 0.0347, and 0.0082 for posterior, mid, and anterior sections, respectively. Figure 33 shows the relationship

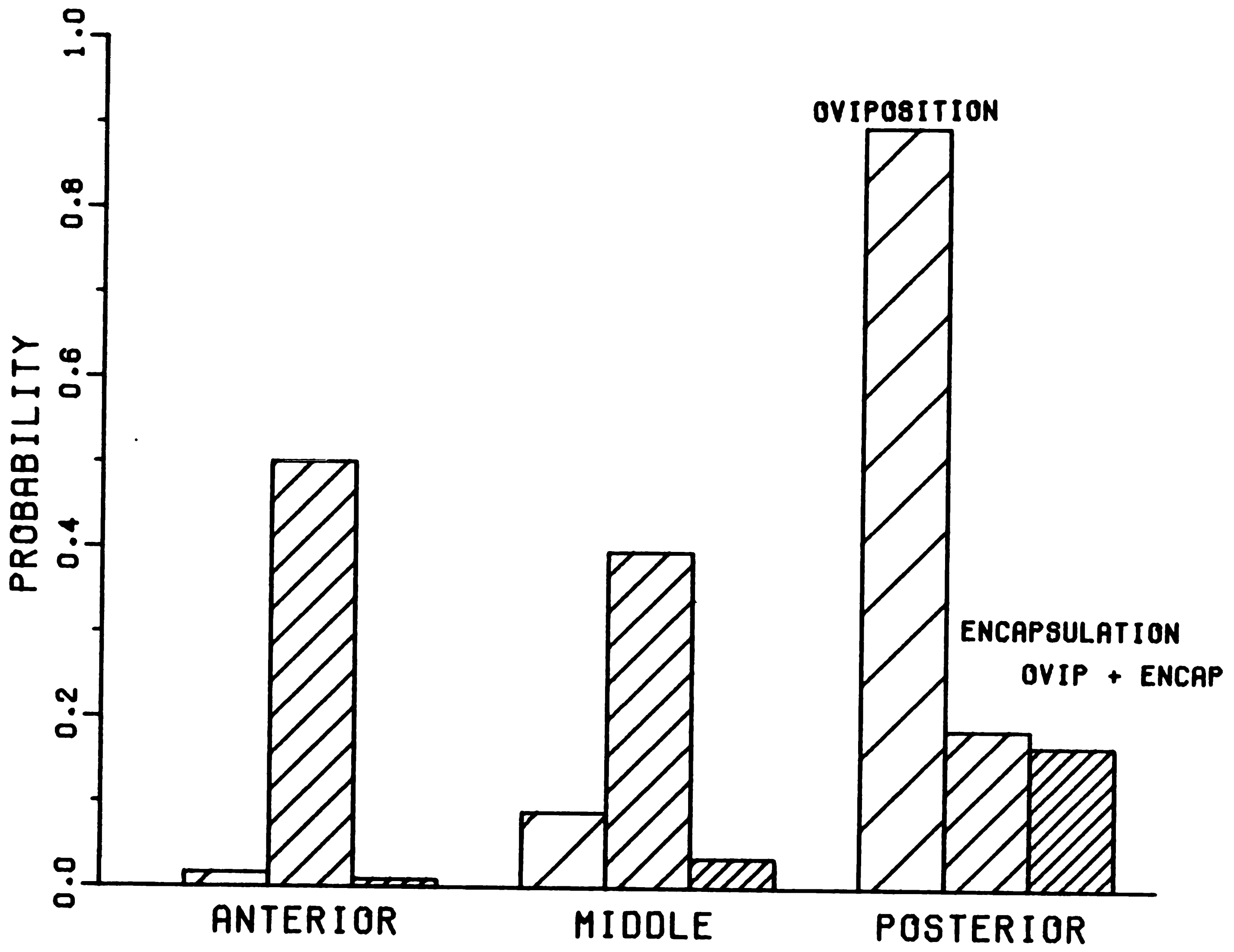


Figure 33. Probability of oviposition and encapsulation for <u>Hyposoter</u> in different portions of a FWW larva.

between the section of the host's body, ovipositional preference, and probability of encapsulation.

The validation of the ETC-FWW system model has produced some promising results. Phenological aspects of the model compared well with field data as did rates of host population increase. The inability to quantify parasites not contained within hosts, however, makes it extremely difficult to track the flow of individuals between host species. This is particularly true for the overwintering period. At this point in time, it is not possible to fully examine the model's performance relative to parasitism and encapsulation and we may only make qualitative inferences based on the general timing and magnitude of events.

Model Sensitivity

Temporal synchrony. The ETC-FWW model, being phenological in nature, lends itself to a series of investigations involving time synchrony relationships. Temporal synchronies have been examined in the past principally at the macro level, that is, considering how parasite and host incidence curves interface. For the most part, these data indicate a positive outcome from varying degrees of asynchrony. The creation of temporal refugia for the host organisms acts as a stabilizing force in long-term relationships (Münster-Swendsen and Nachman 1978). Reasons for temporal coincidence or incoincidence have not been examined to any great extent. From a management standpoint, the restriction of study to the incidence curves rather than causal mechanisms greatly reduces the number of control options. In terms of ecology of parasite-host systems, analysis of incidence curves can only describe the outcome of temporal relations (usually percent parasitism) and the effect on system stability.

Throughout earlier portions of this work, a reductionist approach has been taken. I will continue to utilize these methods here by considering time synchronies as a function of their subcomponents. With regard to the host, its placement in time depends upon the rate that susceptible life-stages enter and leave the system. Therefore, developmental rates of those stages are of importance. In light of this, system responses were examined from the standpoint of altering the host population's developmental characteristics. These alterations were performed through changes in the temperature regime, changes in the population's phenotypic composition (K_p), and changes in species of the host plant. From the parasite's viewpoint, the temperature regime will produce varying emergence patterns. In addition, longevity of adult females increases or decreases the time available for attack activities, as well as the degree of overlap in incidence curves.

Temperature regimes. The effects of different temperature regimes were simulated by obtaining temperature data from 3 different areas in the state of Michigan for 1977: Gull Lake, Houghton Lake, and Marquette (Fig. 34). These data were input into the model as specified earlier. For this series of runs, population densities were initialized with field data from Gull Lake (Table 11) with the frequency distribution of Kp for the FWW derived from field samples. The proportion of individuals in Kp 1 through 10 are 0.0351, 0.1170, 0.1871, 0.2047, 0.1579, 0.1170, 0.0760, 0.0585, 0.0292, and 0.0175, respectively.

As the ETC-FWW system is moved on the south to north gradient, significant changes occur in the temporal synchrony of all 3 populations (Fig. 35, A-C). The Gull Lake simulation demonstrates a very close association between Campoplex and both host species (Fig. 35A). Moving

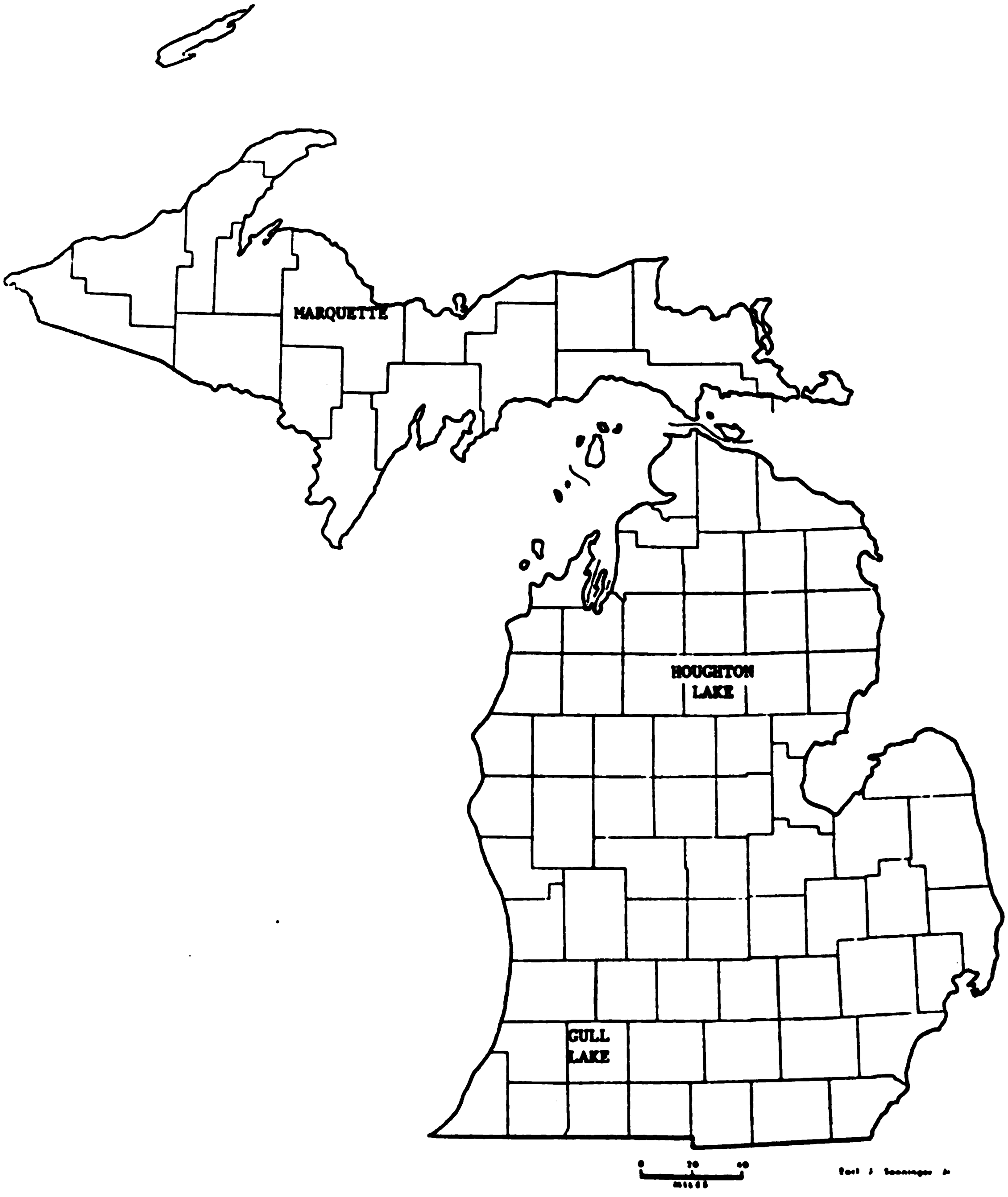


Figure 34. Locations in Michigan for simulation runs.

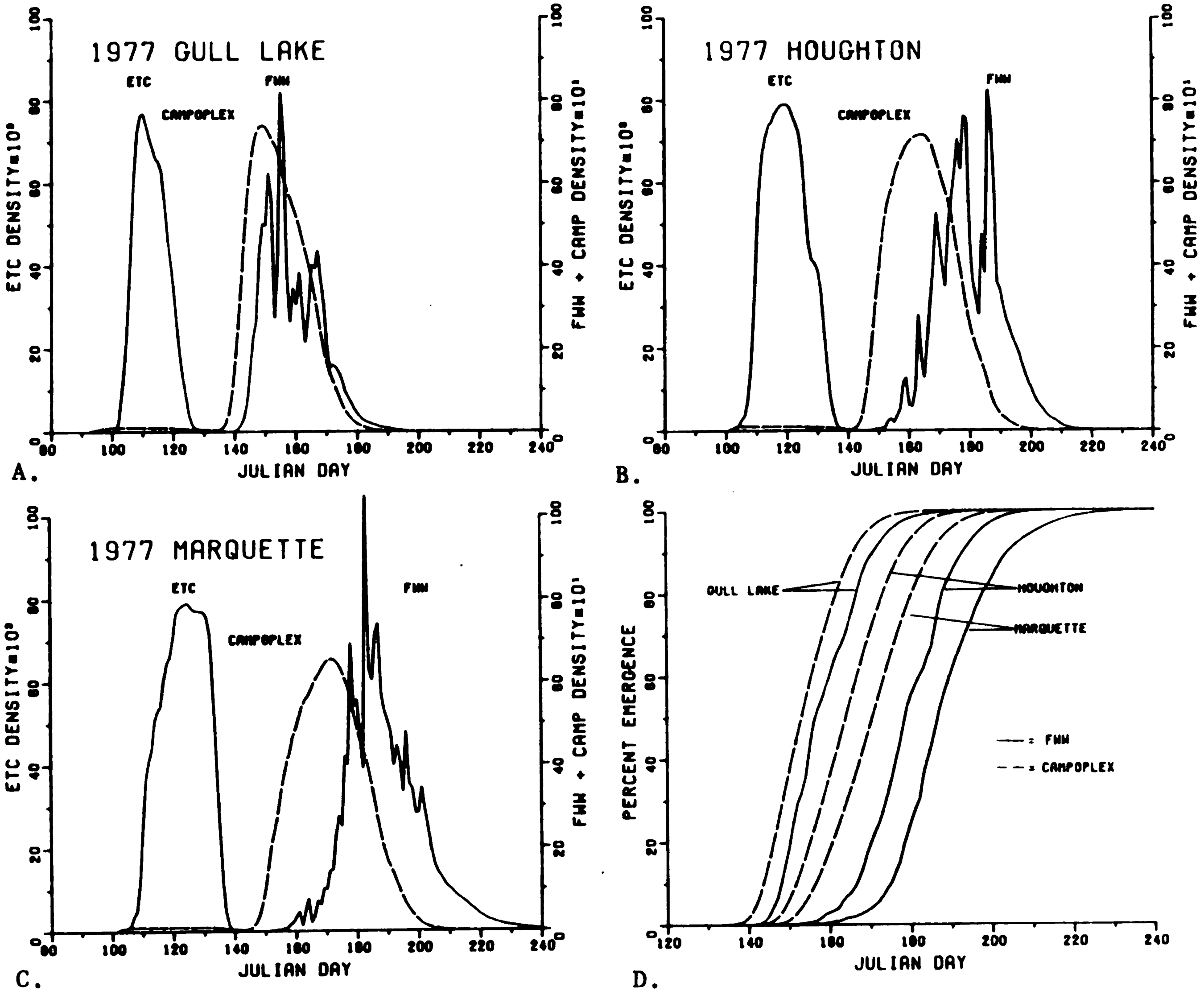


Figure 35. Incidence curves for ETC, FWW, and Campoplex.

to Houghton Lake, a shift in the FWW-Campoplex interaction occurs (Fig. 35B). This shift continues further as can be seen in the Marquette run (Fig. 35C). Figure D allows a direct comparison of each of the runs by plotting cumulative percent emergence curves for Campoplex adults and the webworm larvae over time. The movement toward asynchrony is a direct result of differences in developmental temperature thresholds. Campoplex's base of 42° F (5.56° C) allows it to accumulate more degree-days than the webworm whose base is 51° F (10.56° C). This will most affect populations in cooler temperature regimes where Campoplex pupae will develop during periods of quiescence in the FWW.

As expected, parasite production decreases on the south to north gradient. At Gull Lake, 772 Campoplex pupae were generated from attacks on ETC, and 916 from the FWW. Houghton Lake produced 751 and 923, while Marquette produced 699 and 897 from the ETC and FWW, respectively. Though the trend in declining parasitism is apparent, it does not reflect the extent of asynchrony shown in Figure 35D. Reasons for the smaller than expected decrease in parasitism with high levels of asynchrony are not clear. The most feasible explanation lies in a high ratio of hosts to parasites, presenting low densities of Campoplex with a seemingly endless supply of susceptible larvae. Each adult parasite may attack the maximum number of webworms that it possibly can.

It is not known whether this shifting phenomenon actually occurs under field conditions. The assumption is that characteristics of all 3 populations remain constant as one moves to different geographic areas. As shown earlier in this study and in Morris' work (Morris 1971, Morris and Fulton 1970a,b), emergence patterns may change annually and with geographic location primarily in response to temperature, precipitation and related food quality. Thus, the simulated results may be applicable only under situations where these other selective forces are minimized. Some credence is, however, lent to these simulations in that Campoplex is synchronized with the early portions of FWW populations in New Brunswick and areas inland (Morris 1976). This also occurs in the model for Marquette which is approximately at the same latitude.

From a management standpoint the resultant asynchrony on the south to north transect may have both positive and negative results. A positive outcome is that the opportunity exists to implement additional control options for later emerging portions of the FWW population. However, on the negative side, if asynchrony is severe enough that little impact can be made on the host (pest) population, then one must resort to a series of manipulations favoring later emergence of Campoplex. Further, if the system is relatively insensitive to these changes, examination of alternative management techniques may be warranted.

Effects of phenotypic composition in the fall webworm. In an earlier section, I alluded to the idea that the phenotypic (genotypic) composition of a webworm population may play an important role in parasite production. In turn, the amount of parasite pressure placed on the ETC in the following season may be largely dependent on the distribution of webworm phenotype. This idea can be tested in simulation by varying the frequency distribution of Kp in the FWW. Four distributions were examined emphasizing early, middle (a normal distribution), and late portions of the population, as well as an equal number of individuals in each Kp class (Fig. 36A). The total number of FWW input was 10,000 with an equal number of ETC and 10 Campoplex pupae for spring initialization.

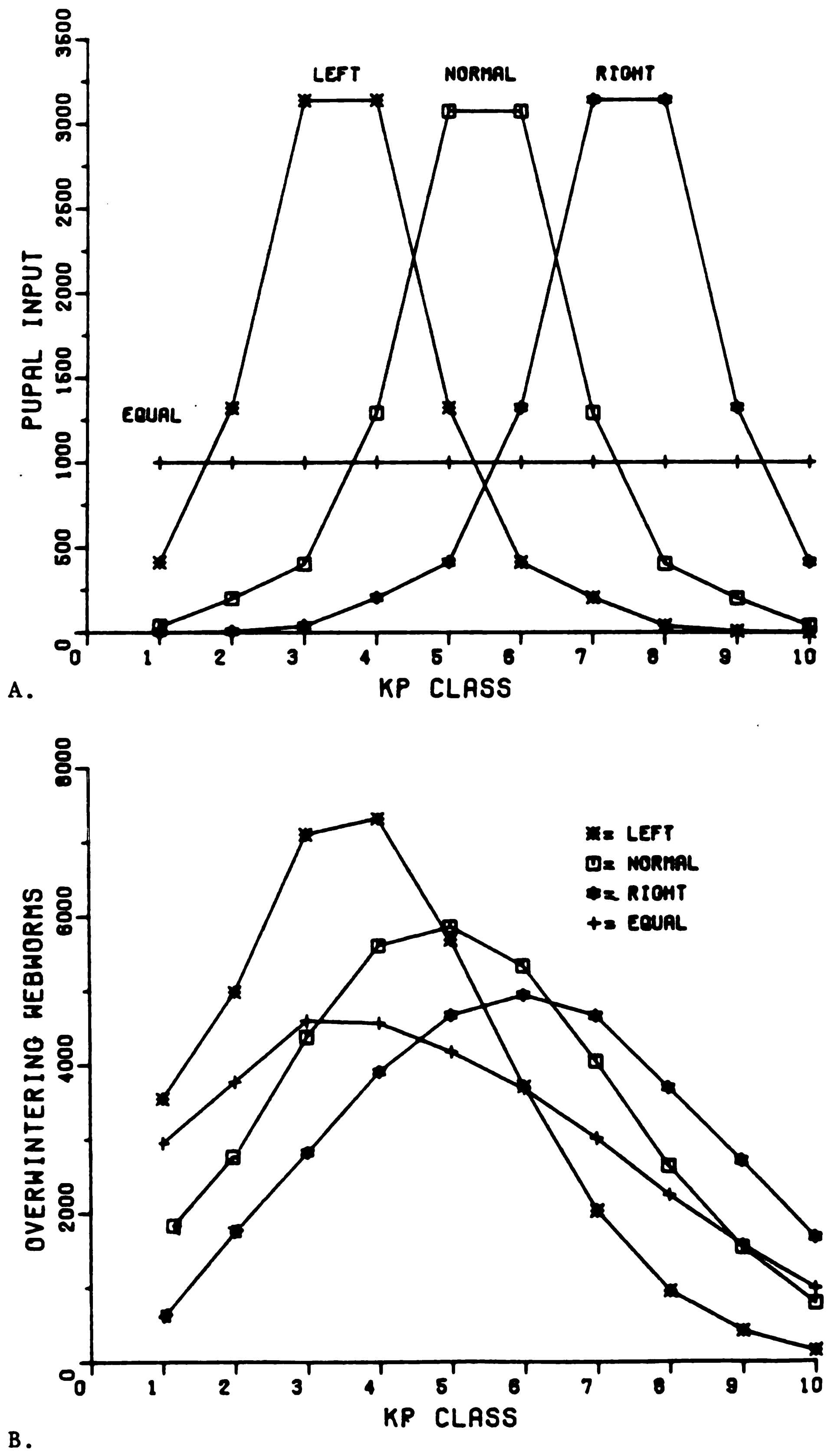


Figure 36. Input/output relationship for effects of phenotypic composition in the FWW.

Figure 36B shows how the composition of the population can change after a single generation. Because of differential fecundity and encapsulation, selection tends to favor those individuals in the first 5-6 Kp classes. Therefore, the Kp distribution changes as a result of varying fitness characteristics. In the distribution skewed LEFT, little change occurs. However, the mode for NORMAL and RIGHT distributions shifts by 1.0 and 1.5 Kp classes, respectively. The EQUAL distribution assumes the pattern of fecundity and peaks in classes of 3-4. Were this trend to continue for another 3 generations, each of these populations would assume the frequency distribution similar to EQUAL and LEFT treatments.

These results are somewhat counter-intuitive in that a mortality agent (Campoplex) appears to be contributing to forcing its host into a higher degree of synchrony with parasitism. One would expect the webworm to opt for a strategy of avoidance as in the RIGHT treatment. However, the ability to encapsulate parasite eggs and reproduce more rapidly, outweighs parasitism. Therefore, the webworm coexists with Campoplex rather than avoiding it and compensates for parasitism through its capacity to increase. In fact, if we compare the numbers of parasites and FWW colonies produced, little change occurs in colony production for each distribution treatment (Fig. 37). In terms of Campoplex significant differences occur with over an 85% decrease in pupal production. The mechanisms involved are compensatory in nature and involve encapsulation, fecundity and temporal avoidance, depending on synchrony with the adult Campoplex incidence curve.

With reference to the system as a whole, the distribution of phenotype (genotype) plays a large role in ETC parasitism and resultant

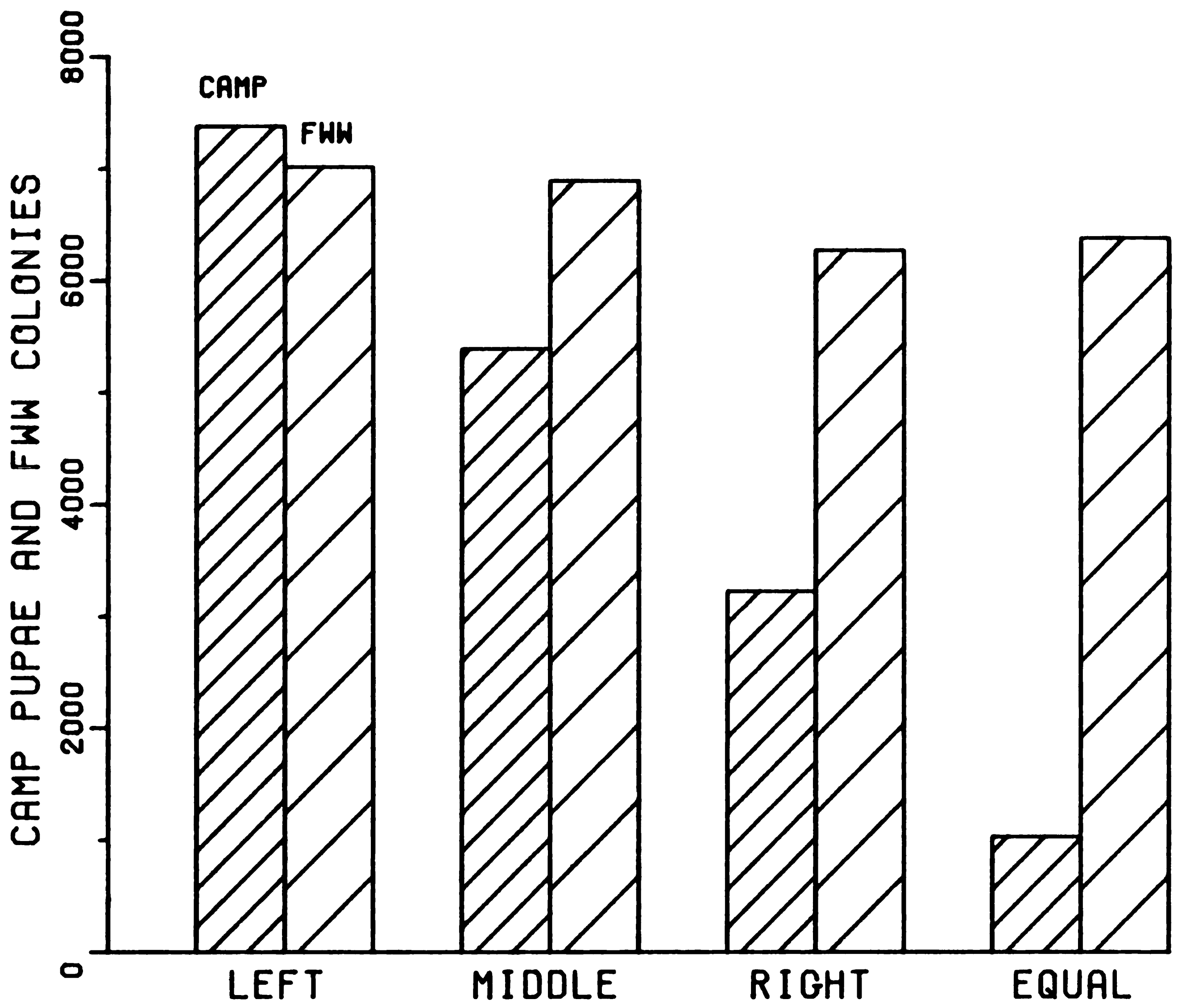


Figure 37. Pupal production for the FWW and *Campoplex* as a function of phenotypic composition in the FWW.

parasite production 2 generations removed. As the distribution becomes skewed to the right, fewer parasites are produced to attack the ETC. In terms of pupal production, the FWW is little affected by its own phenotypic distribution. The tent caterpillar, on the other hand, experiences increased parasite pressure.

A factor which has not been discussed explicitly but is an underlying mechanism in selection for early emerging webworms is food quality. It has been shown that Kp is under genetic control with early individuals begetting early individuals. The aspect of timing with wild black cherry was also shown to favor those individuals with low Kp. Year after year, this situation will hold true even though in certain seasons conditions allow latter portions of the webworm population to expand in time. When compared with a sporadic mortality factor such as parasitism, it is not surprising to see selection for temporal avoidance overridden by the need for high quality foliage. Throughout Morris' (1976) study of parasitism, the encapsulation is implied to be under genetic control. This may be true, but only to the extent that time of emergence (Kp) will directly determine food quality and the amount of stress placed on larvae. Larvae which are under greater nutritional stresses (high Kp) would have a more difficult time in allocating energy to encapsulation than those which are not (low Kp). This does not necessarily mean that encapsulation is independent of individual host differences (genetic), but these differences are masked by the interaction of emergence and quality of foliage. The encapsulation coefficients used in simulation (Table 8) may actually be an assay of nutritional stress as opposed to directional selection combatting parasitism.

As with the series of runs examining geographic variability, phenotypic variability may also play a role in determining the makeup of management systems. Selection forces other than parasites determine a population's susceptibility to parasitism. Thus, the mere determination of pest density will not only have little to do with resulting parasitism rates, but also restrict management options to those which affect the pest population as a whole. Strategies which utilize population structure represent a class of options not used to date. In the following section I will analyze the effects harvesting strategies aimed at predetermined portions of the webworm population.

Harvesting strategies. Phenotypic composition in the FWW was shown to significantly affect parasite production. This composition, however, was varied only in the initial stages of the growing season. The question here is "What effects do explicitly timed harvests have on webworm and _Campoplex_ production?"

The model was initialized with 10,000 ETC, 10 _Campoplex_, and 10,000 webworms distributed in proportions determined from Gull Lake 1977. Survivorship larval stages of the FWW were decreased to 99% throughout a specified time interval (in degree-days). By doing this, an impulse-like, timed, mortality factor was introduced into the system, much like a short residual pesticide. Performance of the system was evaluated with reference to the numbers of FWW colonies and _Campoplex_ pupae generated in the succeeding generation (T + 1).

If the system is evaluated with reference to the number of parasites, then it is possible to actually increase parasite production by harvesting very early in the webworm larval incidence curve. Figure 38A shows the relationship between time of harvest and parasites in the next generation

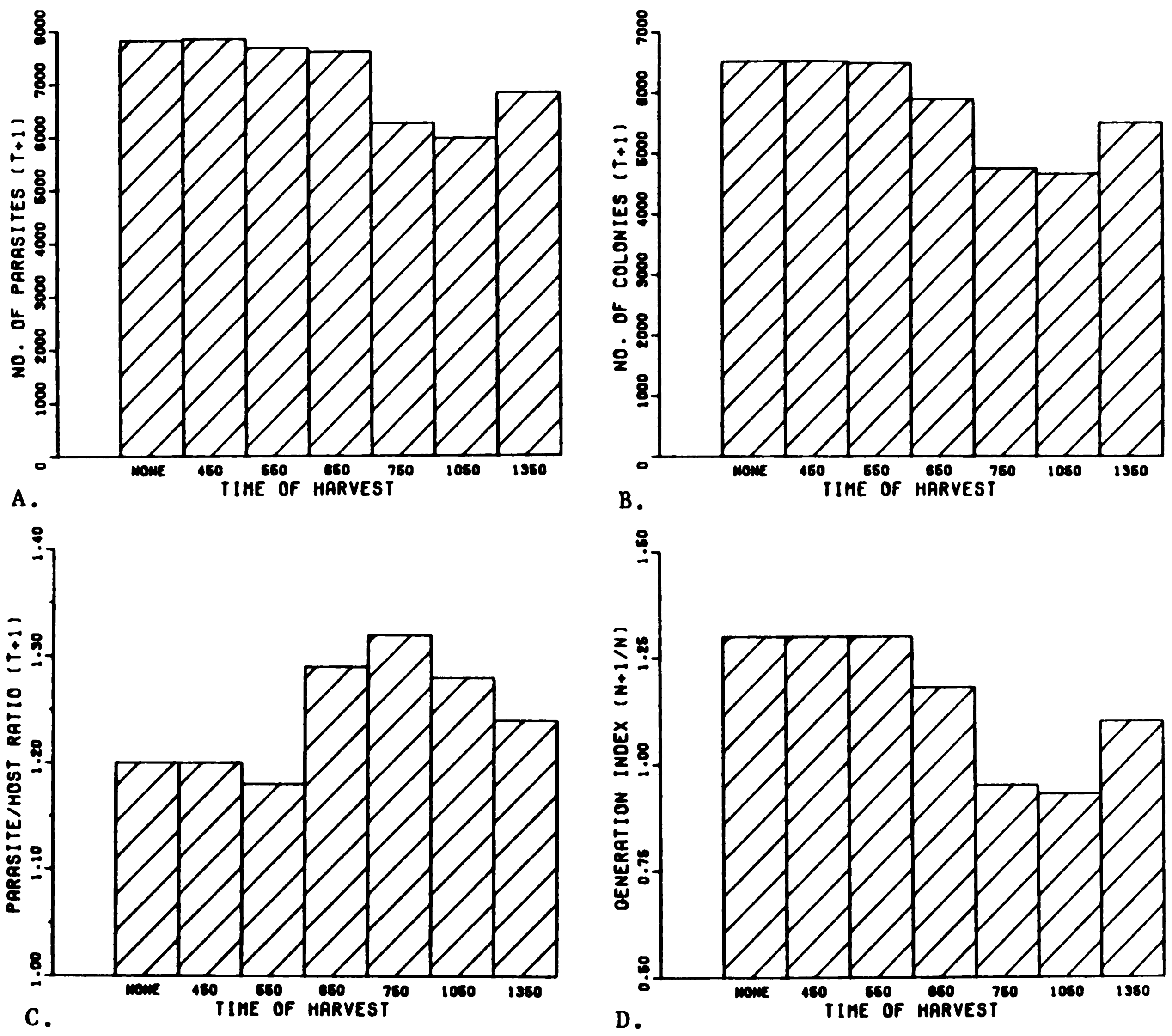


Figure 38. Effects of time of harvest on pupal production, parasite/host ratio, and generation index.

(T + 1). The increase at the 450 D-D_{11} harvest, though not large, suggests that early portions of the FWW population (low Kp) are selected against. Thus, individuals with high encapsulation ability are removed from the population. By doing so, the webworm's susceptibility to parasitism is increased. Because the 450 D-D_{11} harvest occurs so early in the season, only a small portion of the FWW larvae are affected. Thus, there is virtually no affect on colonies produced (Fig. 38B).

In terms of parasite increases relative to host increase, harvesting later in the season maximizes Campoplex, while minimizing FWW population growth. This aspect is shown in Figure 38C with the largest ratio of parasites to hosts occurring at a 750 D-D_{11} harvest. Here, much of the webworm's reproductive capability is removed with Campoplex able to increase at a greater rate. In fact, in all previous harvesting strategies the generation index (i.e., colonies in the following generation/colonies in the previous generation) for FWW was greater than 1.00 indicating population increase. Here, the index drops below 1.00 indicating population decrease (Fig. 38D).

Again, the model suggests that variability throughout the webworm population produces significant differences in response to parasite attack and indirect effects on ETC populations. Further, it was shown that the phenotypic composition of FWW populations produces a larger affect on overwintering Campoplex populations than on the webworm itself (a host-host interaction). Similarly, this host-host interaction will be seen in strategies which manipulate only ETC numbers.

Numerical sensitivity to ETC densities. Numerical sensitivity refers to how the system responds to changes in host-host and parasite-host density relationships. One explicit assumption of the model is that parasite pressure applied to the webworm is dependent on parasite production in the ETC. Thus, it is desirable to examine this interaction from the standpoint of varying ETC populations and determining the impact of the FWW.

In order to evaluate the interaction, the model was initialized with 10,000 webworms (1,000/Kp class), 10 parasites and ETC densities ranging from 5,000 to 50,000. Because temperature is considered explicitly in the parasite attack function, simulations were run using a maximum temperature of 70° F (21.11° C) and a minimum of 50° F (10° C) for each day simulated. This was done to remove any variability caused by spring and summer temperature regimes.

Continual additions to the ETC population results in a saturation of the parasite production curve (Fig. 39A). Inputs of tent caterpillars after 40,000 (ca. 182 colonies) produce no significant increases in second generation parasites. Similarly, there were no significant gains in overwintering Campoplex after this point (Fig. 39B).

The decreasing rate of Campoplex production is particularly dynamic when viewed with reference to the 10 Kp classes in the webworm. Figure 40 shows these responses with classes 2-5 most sensitive to changes in ETC density. Reasons for this lie in the interaction of differential fecundity, encapsulation and Campoplex-webworm synchrony. As second generation Campoplex are augmented through the addition of ETC, the magnitude of the parasite incidence curve increases to better synchronize with FWW larval incidence and increase parasite pressure.

Thus, a viable management option may revolve around the augmentation of ETC populations and any factors which can be manipulated in the one-to-one interaction of Campoplex and ETC or FWW. Techniques which allow

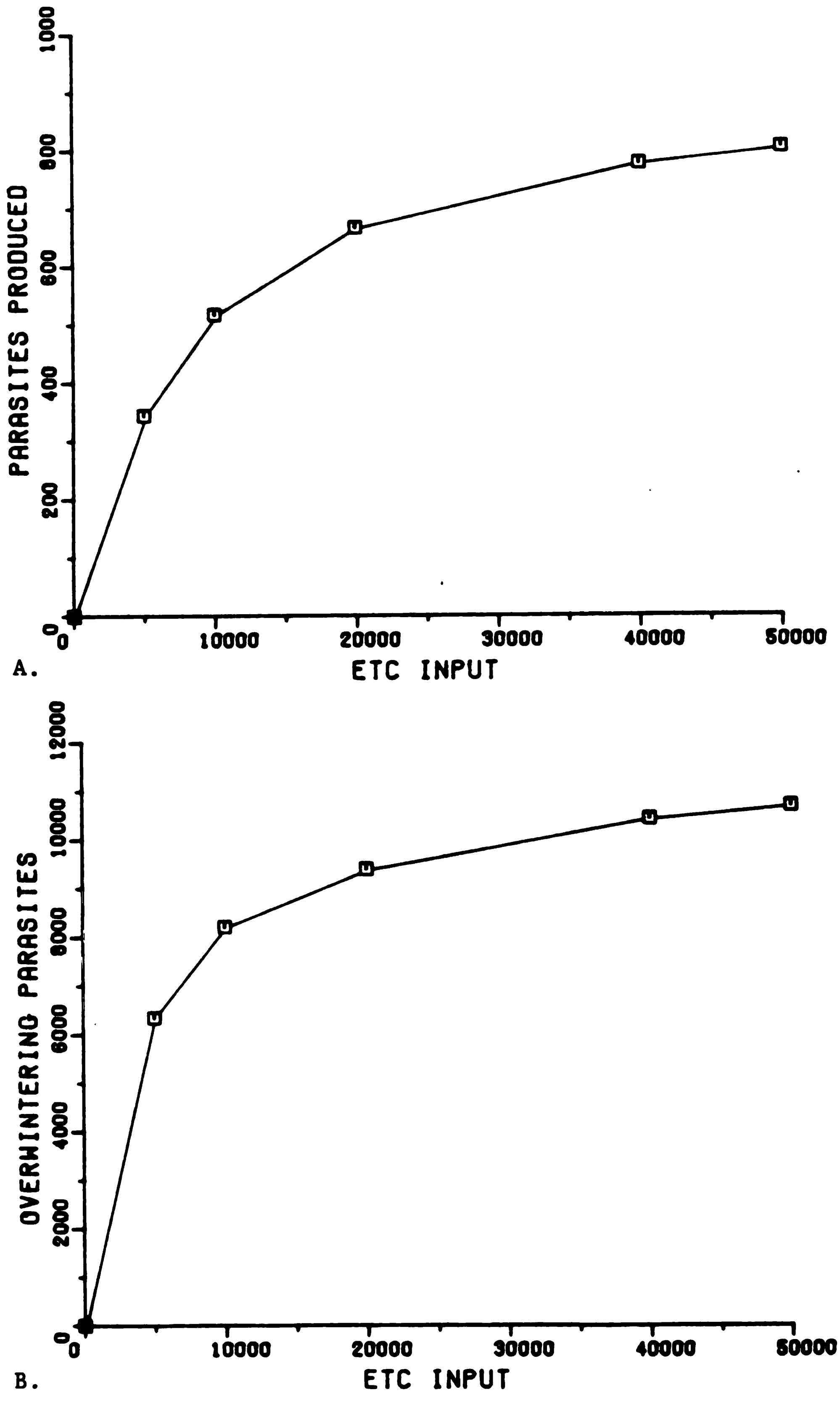


Figure 39. *Campoplex* production in response to varying ETC densities.

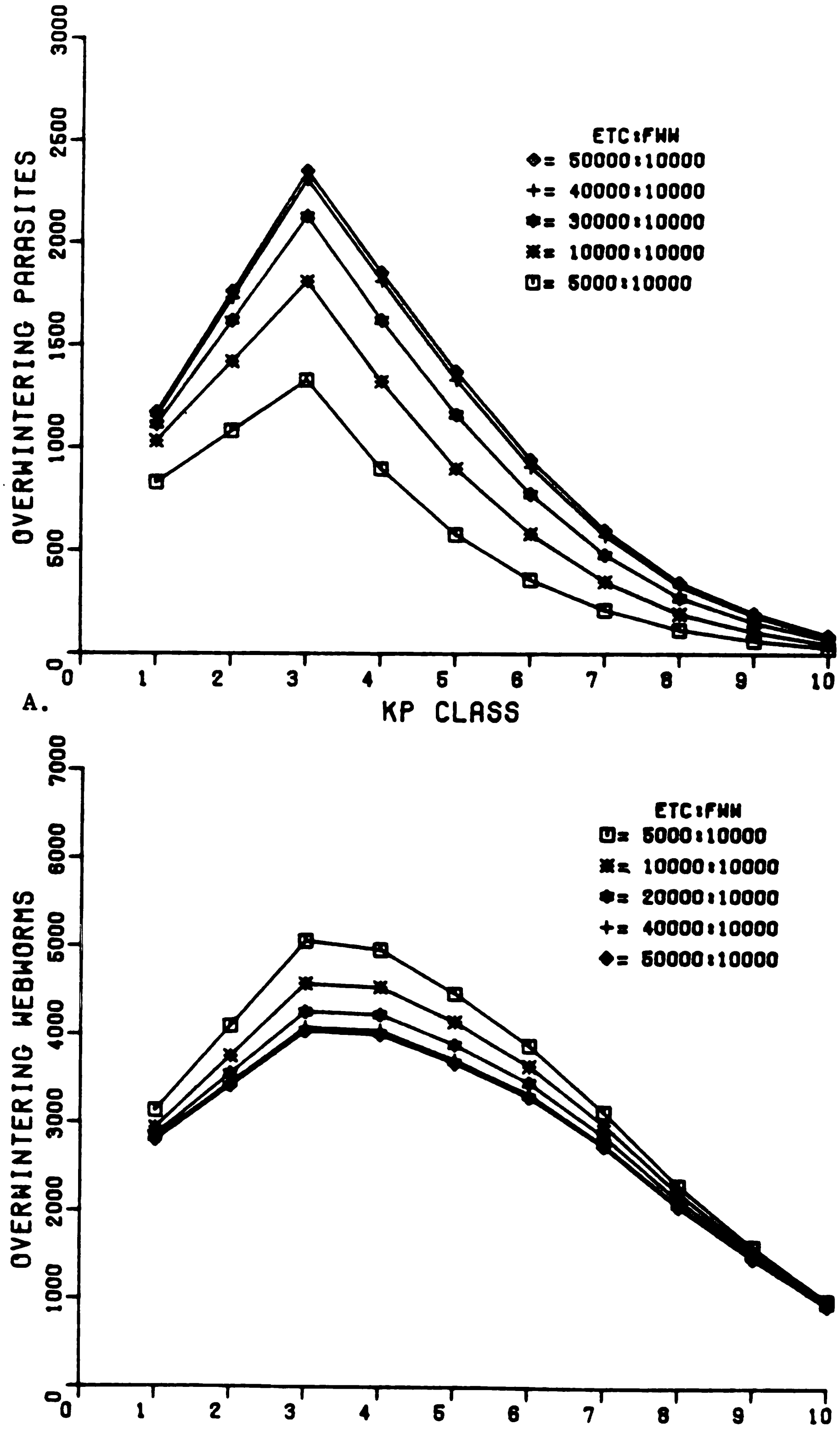


Figure 40. Fall webworm population response to varying ETC inputs.

parasites to spend more time in contact with susceptible host life-stages (i.e., developmental rates of host larvae and adult parasite longevity) are two such options and will be examined in the following sections.

Host plant effects on development and parasitism. Plants directly affect developmental rates of herbivores. The FWW is no different with significant changes in the amount of time spent in each larval instar (Kovacević 1954). In turn, synchrony of parasite susceptible life-stages with adult parasites should be affected. Two extremes in slow and fast larval development were examined for the FWW reared on apple (*Malus pumila* Mill.) and maple (*Acer saccharum* Marsh.). Data for these runs are presented in Table 13.

Results suggest that as more time is spent in susceptible instars, higher rates of parasitism occur. Of those webworms reared on apple, 19.35% of the larvae were parasitized. For maple, there was 24.69% parasitism. Increases in developmental time affords parasites more time to locate hosts and increases rates of parasitism. Thus, parasite-host synchrony can be positively affected through the herbivore-plant interaction.

Table 13. Host plant effects on *Campoplex* parasitism in the fall webworm.

	Malus	*Acer*
Colonies (T + 1)	6522	6535
Campoplex pupae	7822	8212
Percent parasitism	19.35	24.69

Parasite longevity and parasitism. In addition to the host's developmental times, adult parasite longevity is a component of synchrony and parasitism rates. Many studies have examined the factors affecting longevity and allude to how it might affect parasitism (Leius 1967; Barney et al. 1969, Fusco et al. 1978, Miller 1977). Typically, data are derived under laboratory conditions and extrapolations are made to field situations. The objective of this series of runs is to assess the system's sensitivity to alterations of *Campoplex's* longevity.

Again, 10,000 ETC, 10,000 FWW (distributed as in Gull Lake, 1977) and 10 *Campoplex* were used to initialize the model. In order to alter the adult's life span, the delay function used in all previous simulations was taken as a liberal estimate (ca. 30 days), then halved and quartered, resulting in longevity ranging from 7.5 to 30 days.

For both the ETC and FWW, an exponential decrease occurred in parasite production. When *Campoplex* was allowed to live for 30 days, 456 parasites were generated from the tent caterpillar, and 7,822 from the webworm. A 15-day life span produced 326 and 2,098, and 7.5 days 8 and 2 parasite pupae for the ETC and FWW, respectively. Therefore, significant changes occur as a result of factors such as food availability, temperature, pesticide intervention, or any variable altering parasite longevity.

CONCLUSIONS FOR THE ETC-FWW SYSTEM

The study of population dynamics includes two basic areas of study, development and survival. Development relates to temporal placement of populations, while survival studies (within generation) attempt to identify patterns and causes of mortality. In the previous analysis, development and survival were examined in two ways. First, the major components of the system (i.e., ETC, FWW, *Campoplex*, *Hyposoter*, and WBC) were examined in isolation. This was done only to the extent that developmental rates could be determined, stage-specific survivals calculated, and patterns of mortality described. In particular, two distinct survival strategies were found in the ETC-FWW system. The ETC synchronized its emergence with high quantity and quality food. Further, because of rapid developmental rates, particularly in instars 1-3, the ETC was able to minimize the length of time that individuals remain in life-stages susceptible to parasitism and other mortality factors. Eighty percent of the year was spent in the egg stage (actually pharate larvae), and it was found that between 85 and 95% of the individuals survived in that stage.

The FWW makes use of variability to disperse mortality throughout the population. Early emerging individuals (adults) initiate colonies on high quality foliage and consequently are more fecund and have a higher fitness overall. This includes the ability to encapsulate parasite eggs and avoid early frosts prior to pupation. Late emerging webworms feed on a lower quality food but temporally avoid parasites such as *Campoplex* so that there is some compensation for decreased fecundity and susceptibility to cooler temperatures. Webworm populations, therefore, respond to environmental pressures through phenotypic variability and spread risk to various types of individuals (Den Boer 1968, Reddingius and Den Boer 1970).

It is virtually impossible to view population processes without relating components. Hence, interactions between the tent caterpillar, fall webworm, and any common parasites (e.g., *Hyposoter* or *Campoplex*) complete the flow of energy within and between growing seasons. Parasites produced by the ETC go on to attack the FWW and other hosts before returning to tent caterpillars the following season. The model that was developed points to a number of factors linking the three components. One of the more intriguing ideas generated is the concept that the phenotypic composition of a fall webworm population can have major impact on parasitism in the tent caterpillar. Determination of host and parasite densities as single numbers is not sufficient to explain the resultant parasitism rates.

Concepts generated in simulation are indeed useful, though as seen in validation comparisons do not always approximate real world phenomena. In this example, the model's greatest use is derived from its inability to make predictions. The fact that increases in parasite production in the FWW can result in decreased attack in the ETC points to further complexity. In this case, system conceptualization makes no allowances for immigration or emmigration processes in the parasite component, and certainly not for other potential hosts. The utility lies in directing future studies to examine these factors along with an overwintering component examining spatial patterns and movement of parasites into host inhabiting areas.

The plant component of the system model is considered implicitly in the stage-specific survivals and developmental rates. However, it is static and by no means impacts the simulated system as it does in the real world. This was seen, to a limited degree, when altering webworm development as a function of host plant species in simulation. One of the largest impacts on the system may be within a species of host plant and effects on the plant by successive feeding of ETC and FWW. Recent studies by Feeney (1975), Haukioja and Niemela (1979), and others show the dynamic aspects of the defoliation-refoliation process. Feeding by ETC and subsequent refoliation will cause changes in the quality of foliage for the FWW and other late season defoliators. This in turn, affects their mortality patterns, fecundity, susceptibility to parasitism, and most importantly, the underlying distribution of phenotype and/or genotype for the population.

Research in the ETC-FWW system has pointed to the need to accept complexity within and between components. This need further points to a new set of system concept requirements not presently adhered to in management systems using natural controls.

DISCUSSION OF CONCEPTUAL NEEDS FOR MANAGEMENT OF PARASITE SYSTEMS

Given both the holistic philosophy promoted throughout this work and information gained in the analysis of the ETC-FWW system, "How is our concept of parasite-host interactions altered?" The following discussion considers different categories of parasite systems and outlines those factors functioning as determinants of parasitism.

Framework for System Conceptualization

Parasite systems in general may be viewed as subsets or simplifications of the conceptual model shown in Figure 41. Here, a generalized succession of hosts is attacked by a parasite pool. Hosts, as well as the parasite pool, may either be represented by single species or a group of species. Further, the magnitude of the developmental time lag (Δt) then determines whether the model applies to a single growing season

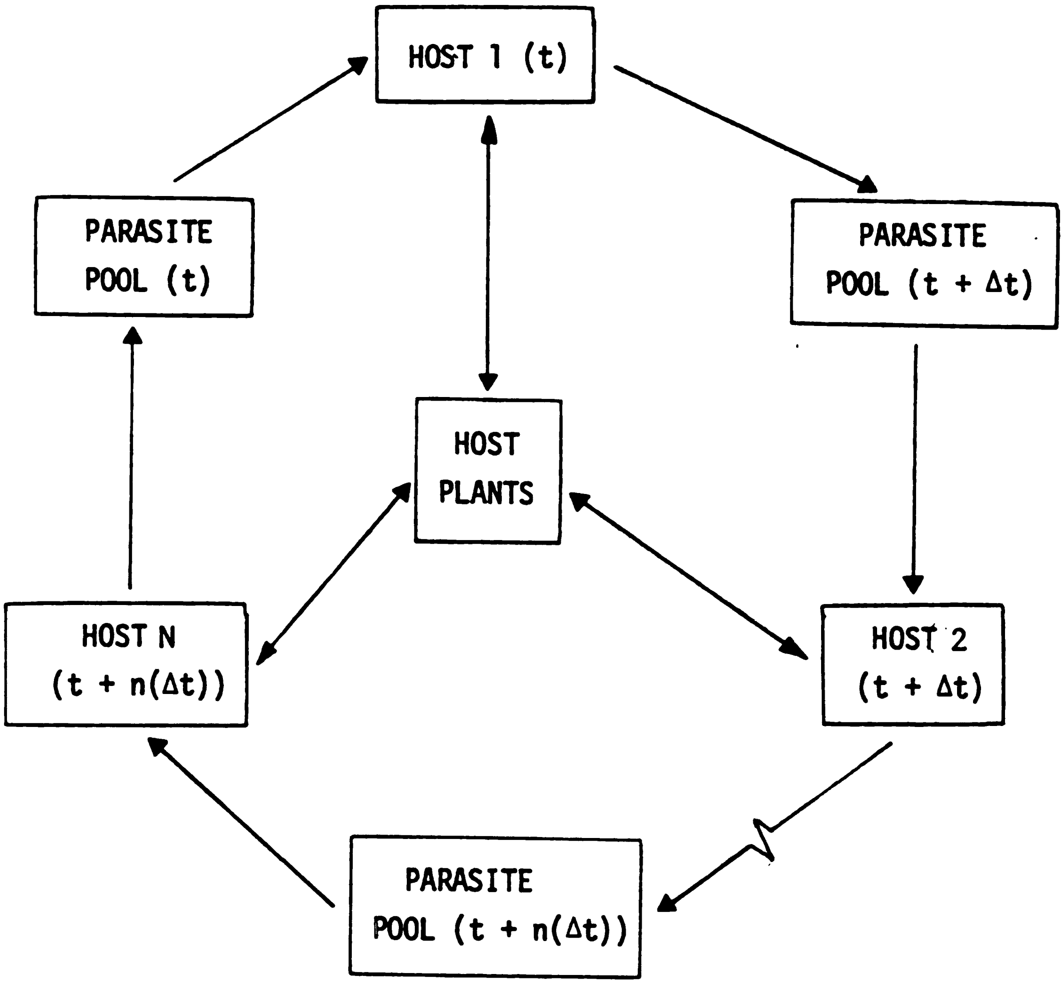
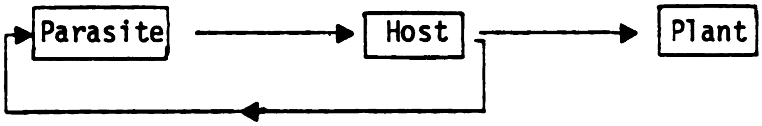


Figure 41. Generalized succession of hosts and parasites.

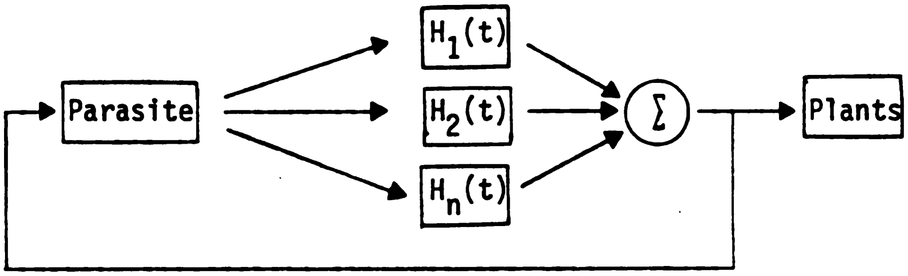
or a series of N growing seasons. For example, Host 1 at time t appears in the spring and is attacked by parasites at time t. After developing in Host 1 the multivoltine species re-emerge to attack Host 2 at $t + \Delta t$. Host 2 is either a second generation of Host 1 or another species. The time period, Δt, represents the developmental time lag for the parasite pool (i.e., length of immature life-stage) and affects their synchrony with Host 2 at $t + \Delta t$. This can be generalized for N numbers of hosts and n time lags (i.e., the parasite pool at $t + n(\Delta t)$ and Host $N(t + n(\Delta t))$. Variations of this generalized model are as follows:

1) single host-parasite systems (SHP) (Fig. 42A),
2) multiple host-parasite systems: synchronous host availability (MHPS) (Fig. 42B),
3) multiple host-parasite systems: asynchronous host availability (MHPA) (Fig. 42C), and
4) multiple parasite versions of 1-3. (This final variation will not be considered explicitly in this study. Considering all of the possible combinations it is felt that the inclusion of number 4 will only serve to cloud the more general concepts behind the determinants of parasitism.)

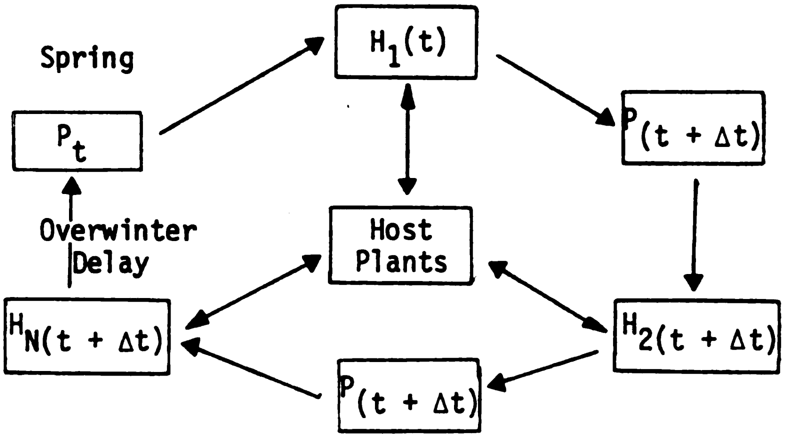
In most cases, parasite competition can be looked upon as an additional mortality factor for immature parasites becoming part of the biotic environment. In addition, little information is available concerning parasite-parasite interactions other than the mortality aspects.



A. Single host



B. Synchronous multiple hosts



C. Asynchronous multiple hosts

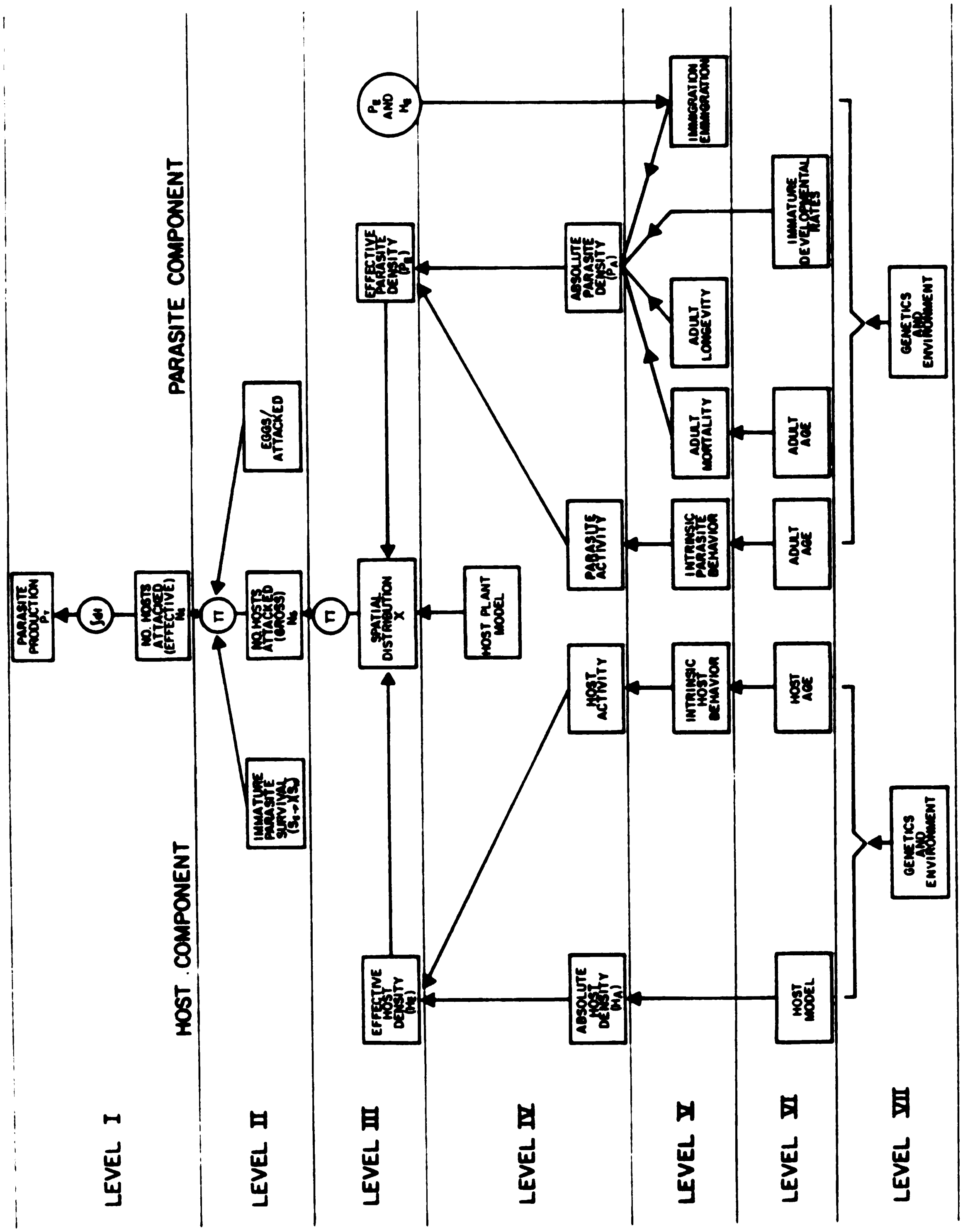
Figure 42. Classes of single and multiple host-parasite systems.

Single Host-Parasite Systems

Single host-parasite systems (SHP) are defined as in Figure 42A and composed of a single species of host and parasites. The basis of parasite-host interaction theory has been developed around this model and serves as a point of departure for more complex systems. One of the more important concepts to be drawn from the SHP model is the idea that the host organism is, to a large extent, responsible for its own fate in terms of parasite pressure in succeeding generations. For an SHP system parasite pressure will only be a function of previous parasitism rates and factors inherent in the host population making it more or less susceptible to parasitism, such as phenotypic/genotypic composition (i.e., self regulation), all other factors being constant. Other factors do not remain constant, however, and must be explored by a within generation basis and formated as in Figure 43.

The within generation components of SHP systems may be viewed as a series of interconnected processes leading to a complex, yet organized, model of the determinants of parasite numbers. This approach is not altogether different from the experimental component analysis of Holling (1963) (i.e., each of the components of a particular process is examined in terms of a set of variables making up the process). "It is based on the belief that the characteristics of any specific example of a complex process can be determined by the action and interaction of a number of discreet components" (Holling 1966). Each of the discrete components (effective and absolute density) are arranged with respect to related components at lower levels (vertical plane), as well as analogous or related processes in horizontal positions of the model (e.g., effective parasite and host density).

Figure 43. The within generation components of SHP systems.


LEVEL I
LEVEL II
LEVEL III
LEVEL IV
LEVEL V
LEVEL VI
LEVEL VII
HOST COMPONENT
PARASITE COMPONENT
PARASITE PRODUCTION
NO. HOSTS ATTACKED (EFFECTIVE)
NO. HOSTS ATTACKED (GROSS)
IMMATURE PARASITE SURVIVAL
EGGS/ ATTACKED
SPATIAL DISTRIBUTION X
HOST PLANT MODEL
EFFECTIVE HOST DENSITY
EFFECTIVE PARASITE DENSITY
P AND N
ABSOLUTE HOST DENSITY
HOST ACTIVITY
PARASITE ACTIVITY
ABSOLUTE PARASITE DENSITY
INTRINSIC HOST BEHAVIOR
INTRINSIC PARASITE BEHAVIOR
ADULT MORTALITY
ADULT LONGEVITY
IMMATURE DEVELOPMENTAL RATES
IMMIGRATION EMIGRATION
HOST AGE
ADULT AGE
ADULT AGE
HOST MODEL
GENETICS AND ENVIRONMENT
GENETICS AND ENVIRONMENT

Each component is dynamic and may change its characteristic value or frequency distribution of values with time. For example, within any given period of an insect generation, the distribution of fecundity throughout the population may change in response to food availability, temperature or the genetics of the population. Ultimately, changes in any component can be traced back to fluctuations in the environment. Environment is defined as that portion of the universe of concern which we do not explicitly include in the model (Tummala et al. 1975). Environmental factors, though usually considered to be of the abiotic type, (temperature, relative humidity, etc.) may also include biotic factors such as, other parasites, predators and pathogens. The performance of the system (adult parasite production) is then a function of the behavior of each of the discrete components, their interaction, and environmental variables driving the system. With these things in mind, the total number of adult parasites produced is an integrator of all variables below it and serves as the performance criterion for the system as a whole. Understanding of within generation dynamics is facilitated when viewing relevant processes in this manner. However, between generation dynamics are not considered. The remainder of this discussion will focus on those intergeneration factors affecting parasite production.

Multivoltine Single Host-Parasite Systems

Let us now examine some multivoltine variants of SHP interactions. Figure 44 graphically illustrates some common systems. Within each of these models, daily parasite-host interactions are determined by the same factors as discussed and presented in Figure 43. However, the dynamics of the system as a whole presents some additional considerations.

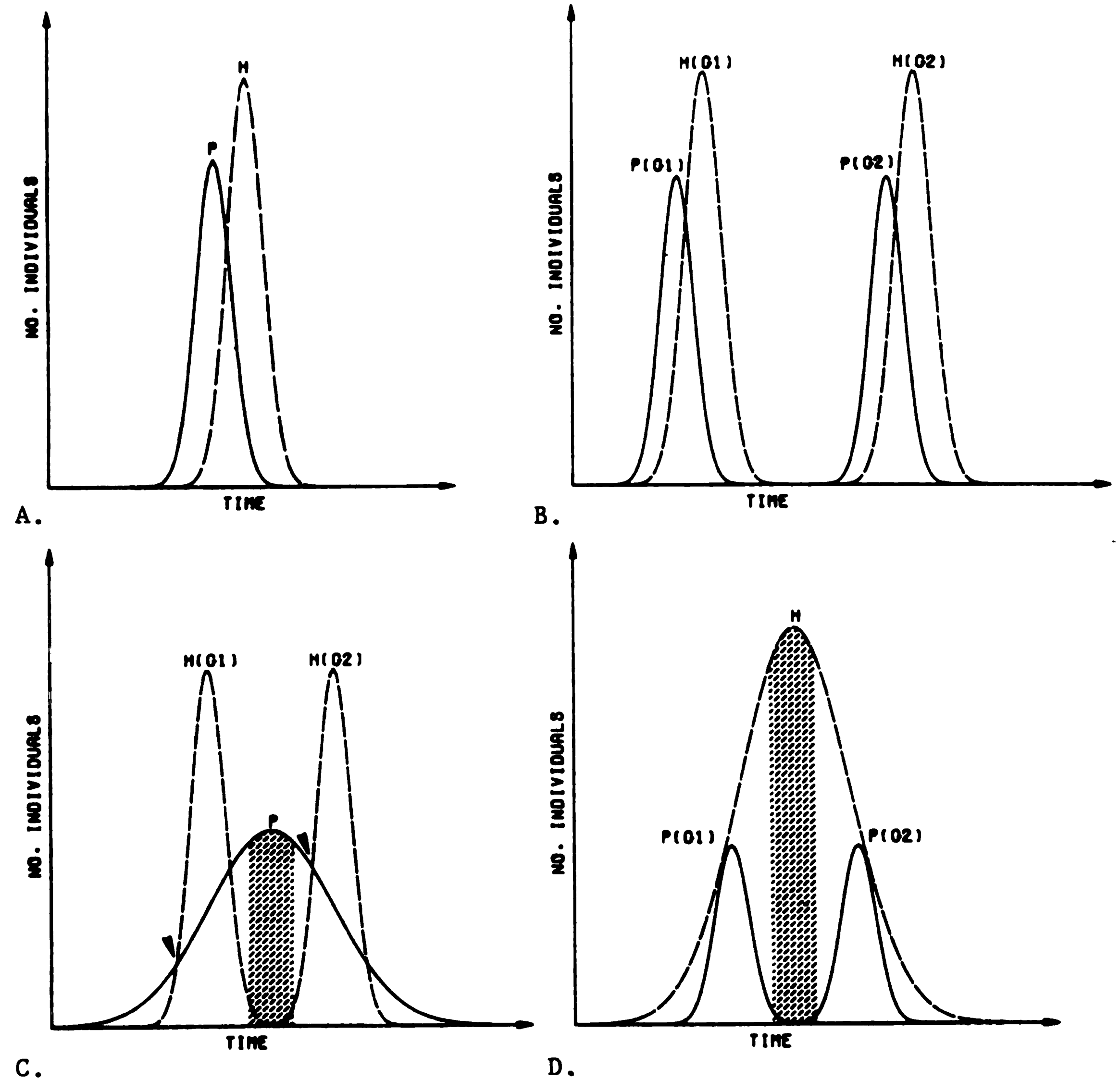


Figure 44. Single host-parasite systems.

Performance relative to a complete cycle must be viewed with reference to an expanded time frame. Referring to Figure 41, a complete cycle is formed when the numbers of parasites produced to attack Host 1(t) have gone through Host 2(t + Δt) and Host N. This alteration in a time frame is not significantly different than our view of single generation SHP systems except that control of the first generation of the host is now not self-regulating. It is dependent on previous generations and their behavior, genetics, and the environment in which they exist.

Closely related to the univoltine SHP system (Fig. 44A) is the multivoltine situation in which the host and parasite remain synchronized on a per generation basis (Fig. 44B). In other words, the length of either the parasite or host generation is not sufficiently large enough to encompass more than a single generation of the other (see Figs. 44C,D).

If it is assumed that the characteristics of each population and the environment were the same for all generations, then there is merely a repetition of the single generation case. However, properties of the system do not remain constant. Changes in environmental factors, such as temperature, can significantly alter parasite production. An example of this is demonstrated with Aphytis maculicornis (Masi), a parasite of the olive scale in California. During the spring Aphytis is highly successful in attacking the scale; however, the summer generation is greatly inhibited by high temperatures and low precipitation (Huffaker and Kennett 1966). An extreme example of this occurs in many agricultural situations. Parasite populations often experience varying levels and types of pesticidal pressure depending on the time of year and geographic location (Huffaker et al. 1962, Rabb 1969, DeBach and Rose 1977).

Changes may also occur in the developmental characteristics and survival patterns of the host. This may be due to either a change in species of host plant or in quality of the host plant and result in asynchrony of both populations and increased mortality (Feeney 1976, Morris 1967).

Another variant of the SHP system is shown in Figure 44C where the parasite's generation time is at least twice as long as the hosts'. The same sort of phenomena that occurred in B may also occur here. Of greater significance, however, is the period of time in which hosts are either at low levels or lacking (shaded area). Parasites attacking during this time must either be well equipped to locate hosts at low levels or perish without being able to deposit progeny. The length of this period is, therefore, a function of three factors: the parasite's ability to locate prey at low levels, the developmental rates of the host and parasite, and environmental factors such as temperature governing the developmental velocity of each of the system's components. In some situations, such as with aphids, the rate of reproduction is so rapid that there may be 3 or 4 host generations for every 1 parasite generation acting essentially as a single generation host (Passlow and Roubicek 1967, Kralifa and Sharif El-Din 1965). Thus, the between generation host lag becomes nonexistent.

Another feature of the multivoltine host system relates to the selective pressure applied to different portions of the host population. In Figure 44C (arrows) hosts which emerge early in the first generation receive comparatively less parasite pressure than late emerging individuals. On the other hand, late emerging individuals in the second generation see comparatively less parasitism. The evolutionary and phenological aspects of this concept are far reaching, possibly moving the system to 2 parasite generations through decreased host availability during the developmental lag period (Fig. 44C, shaded area).

Similar to the multivoltine host example is the multivoltine parasite (Fig. 44D). Here again a developmental lag occurs, in this case, with the parasite component. During this period parasite pressure is at its lowest. Potential hosts occurring in the lag will have a high probability of escaping parasitism. Selectively, the extremes of the host incidence curve will be forced to adapt to the majority of the parasite attack by shifting in phenotypic (genotypic) composition or to accept this differential mortality (Morris 1976). In an applied situation, the developmental lag can be utilized in the application of management strategies which are antagonistic to adult parasites. The cereal leaf beetle system is an example where pesticides should not be applied outside of the lag period or "biological window" (Haynes et al. 1974).

There are other types of SHP systems, however, the ones described above represent a readily identifiable family of interactions. Variations from this basic framework may produce more simple or complex systems.

Multiple Host-Parasite Systems

Multiple host-parasite systems (MHP) are defined as interactions involving one or more generations of a single parasite species and more than one host species (i.e., polyphagous parasites). They are further defined by dichotomizing them into two classes: those with synchronous host availability (MHPS) and those with asynchronous host availability (MHPA).

A synchronous system is pictured in Figure 45A and is composed of a parasite (P) with 1 to N host species (H1-HN). It is synchronous because each of the hosts are occurring, to some extent, at the same point in time with the parasite attacking one or more during that time period.

If the objective of study is to determine total parasite production for such a system, then the problem reduces to that of a SHP system with an extended host generation. However, if objectives involve cause and effect and the differnetial impact on the various host populations, then an SHP system concept will not be sufficient. The first consideration is to determine the attack rates on any one of the HN species while in the presence of the other HN-1 species. If it is assumed that the parasite has no preference for one host over another, then the proportion of H_1, taken over all other hosts will be:

$$\frac{N_1}{\sum_{i=1}^{N} N_i - N_1} = \frac{H_1}{\sum_{i=1}^{N} H_i - H_1} \qquad [33]*$$

where:

N_i = the number of individuals attacked in the i^{th} species.

If there is a preference for H_1 over the other species then H_1 must be more heavily weighted, hence:

$$\frac{N_1}{\sum_{i=1}^{N} N_i - N_1} = \frac{cH_1}{\sum_{i=1}^{N} H_i - H_1} \; . \qquad [34]$$

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*Equation 33 and the following discussion are modified from the work done by Murdoch and Oaten (1975).

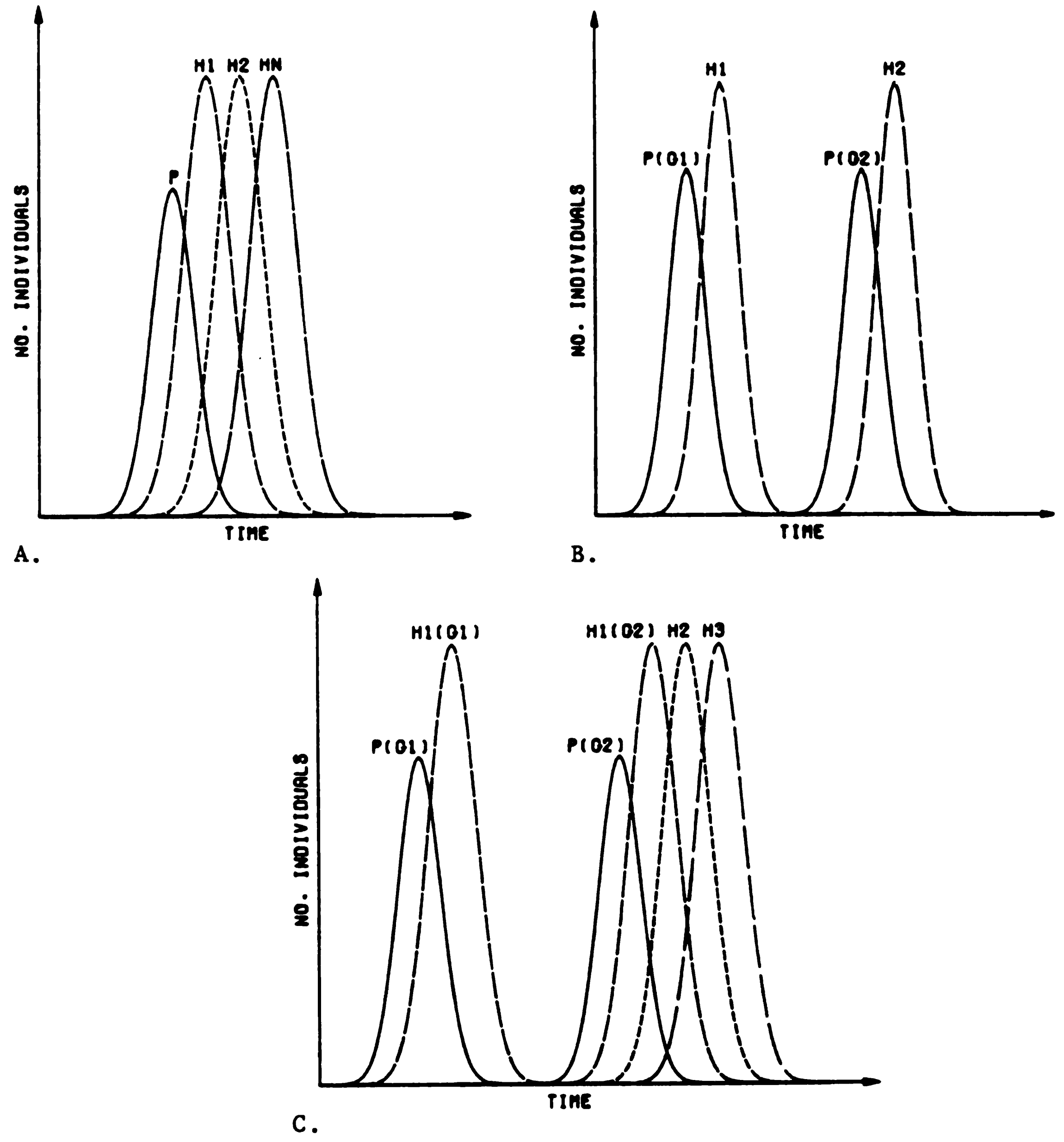

Figure 45. Multiple host-parasite systems.

For H_1 preference, the coefficient c will be a constant greater than 1. If H_1 is preferred less than the other species, c will be less than 1.

Assume now that c is not a constant and that it is an increasing function of $H_1/\sum_{i=1}^{N} H_i - H_1$. In other words, the number of H_1 taken becomes proportionately greater as the numbers of H_1 increase relative to the other hosts. As the frequency of H_1 changes relative to the other host species, the parasite begins to spend a disproportionate amount of time attacking H_1. This concept is termed "switching" (Murdoch 1969). Therefore, P_1, the proportion of the total hosts attacked, is:

$$P_1 = \frac{cH_1}{cH_1 + \left(\sum_{i=1}^{N} H_N - H_1\right)} . \qquad [35]$$

Letting the proportion of H_1 in the total host complex be F_1, then:

$$P_1 = \frac{cF_1}{1-F_1+cF_1} . \qquad [36]$$

If c is assumed to be a linearly increasing function of $H_1/\sum_{i=1}^{N} H_i - H_1$ then:

$$P_1 = \frac{cF_1^{\,2}}{(1-F_1)^2+cF_1^{\,2}} \qquad [37]$$

The resulting family of curves appears as in Figure 46 with curves A and B demonstrating no preference at unity (i.e., 50:50) and C and D demonstrating preference for hosts other than H_1. In curve C, for example, $F_1 = .5$ and $P_1 = .2$, thus, even though H_1 makes up 50% of the host complex, the attack rate on H_1 is less than unity.

Throughout the above discussion the models have only included what might be called <u>frequency dependent</u> responses. In other words, any change in attack rate N_i as a function of H_i or the total potential host population $(\sum_{i=1}^{N} H_i)$ is ignored. Murdoch and Oaten (1975) have approached

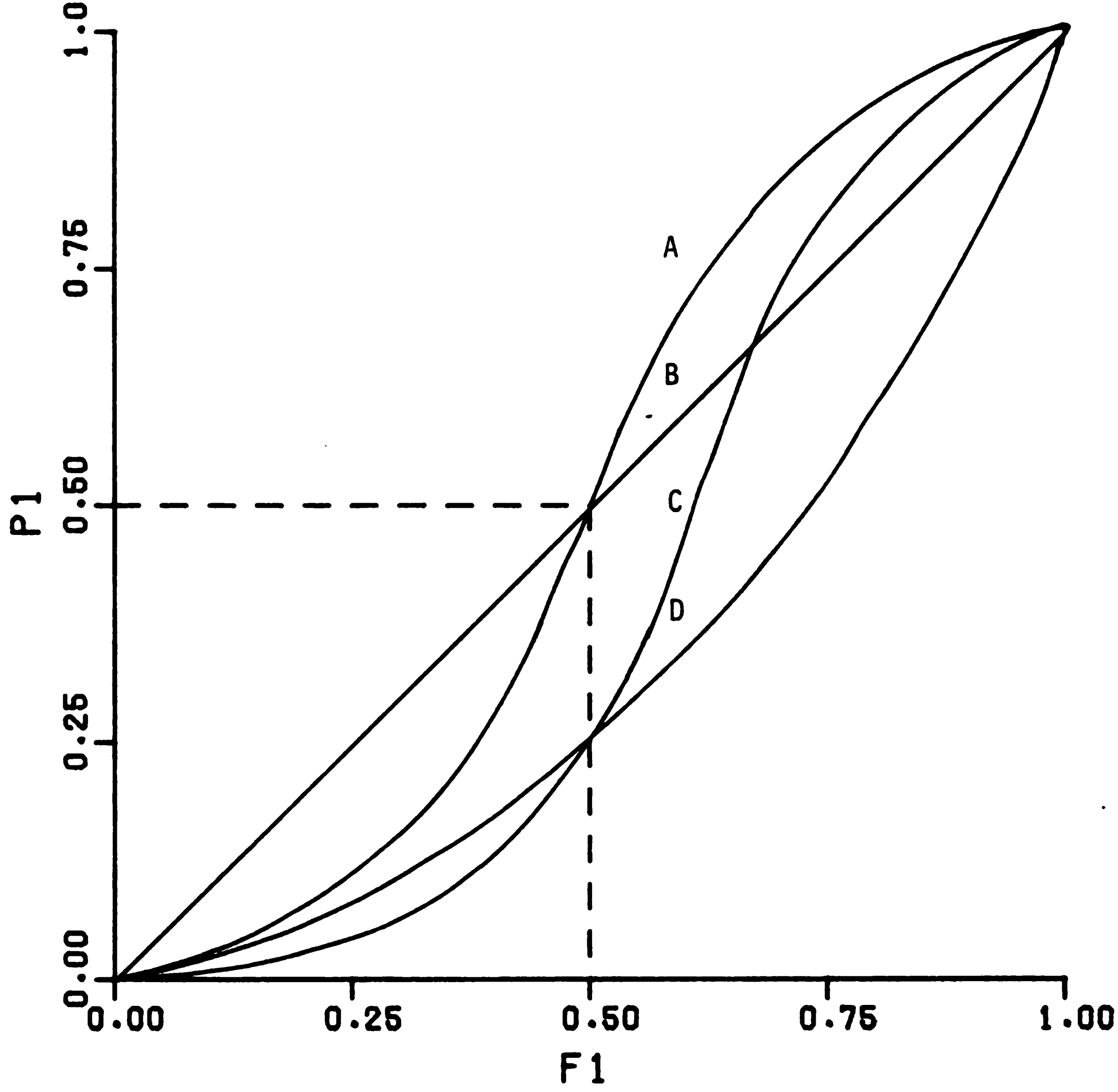

Figure 46. Proportion that H_1 forms of P_1 versus the proportion it forms of total hosts (prey), F_1 (taken from Murdoch and Oaten 1975).

this problem using two methods, the first of which will be discussed. Using this method, an existing attack model was modified to include N host species and preference coefficients. The Holling "disc equation" (1959) is used as an example where the gross attack rate per parasite for a single host is:

$$N_G = \frac{aTH}{1+aT_hH} \qquad [38]$$

where:

H = the host density,

T = the total time available for attack,

a = the attack rate as defined by Holling (1965, 1966), and

T_h = the handling time, which for parasites is a function of the time spent pursuing and attacking or ovipositing (larvipositing) in or on the host.

Modifying the above model for a MHPS system for i hosts we obtain:

$$N_{Gi} = \frac{a_i T H_i}{1+\sum_{i=1}^{N} a_i T_{h_i} H_i} \qquad [39]$$

(Murdoch 1973). This model holds if host species are attacked independent of one another. Incorporating frequency dependence into the model produces:

$$N_{Gi} = \frac{\alpha_i F_i H_i T}{1+\sum_{i=1}^{N} \alpha_i F_i H_i} \qquad [40]$$

Here, switching is incorporated into equation 39 by assuming a_i to linearly increase with the proportion of the total host population occupied by the ith species or:

$$a_i = \alpha_i F_i \qquad [41]$$

where:

$$F_i = \frac{H_i}{\sum_{i=1}^{N} H_i} \qquad [42]$$

and α_i is a constant for the ith species. The model becomes:

$$N_{Gi} = \frac{\alpha_i F_i H_i T}{1 + \sum_{i=1}^{N} \alpha_i F_i T_{h_i} H_i} . \qquad [43]$$

The models discussed above have been developed primarily for use in predator-prey systems. However, the concepts are largely applicable to parasite-host systems. Empirically little is known about the dynamics of switching in MPHS interactions. Studies have centered on laboratory examination of host preference and density relations, while frequency dependency has not been dealt with. On a one parasite-one host basis, factors which are of importance in the host selection process are size, color, movement and a number of other physical factors (Vinson 1976). A conceptual model of how these factors interact with parasite behavior and environment is presented in Vinson (1975). Aside from the confounding effects of frequency dependence and possible host switching, one-to-one models of host selection such as Vinson's are, however, probably valid.

Another factor which separates MHPS from SHP systems in this context is preimaginal conditioning. This relates to preference for one species over another based on the host that a parasite was reared on. Preference is defined in terms of the actual selection process, changes in fecundity, production of female progeny, and searching behavior (Vinson 1975, Legner and Thompson 1977, Taylor and Stern 1971, Marston and Ertle 1973).

In MHPS systems host preference is not only due to physical characteristics of each host and its microenvironment along with frequency dependence, but is also due to conditioning of the previous generation. Attack of a particular host species may, therefore, be mediated by preimaginal conditioning and either strengthen or weaken preferences with each succeeding generation. These factors along with frequency and density dependence play a unique role in MHPS systems not found in single host-parasite systems.

The second class of MHP interactions is the asynchronous system (MHPA). An asynchronous system is pictured in Figure 45B and is made up of a multivoltine parasite with different host species separated in time.

The within generation dynamics of an MHPA system does not differ from its single host counterpart (Fig. 44B) in that there is still only a one-to-one interaction of populations. However, the between generation dynamics are different due to spatial, temporal, and behavioral characteristics of the different hosts which affect parasite production. The second generation host and parasite are not only affected by conditions at that point in time but are "preconditioned" by system and environmental parameters in the first generation.

An interesting variant of the MHPA system is a combination of synchronous and asynchronous host availability (Fig. 45C). Here, aspects of preimaginal conditioning may play an important role in the amount of parasite pressure applied to a particular host. If preimaginal conditioning does occur, and there are at least 2 generations of one host, preference in the second generation will be a function of frequency, density, and parental host. However, parasite production in the first generation will only be a function of density, and of course, the full range of factors covered in SHP systems.

At any point in time in a MHP system, parasitism is dependent on the one-to-one interactions of parasite and host. However, when viewed in a larger time frame, changes in the components of the system significantly alter the parasite's performance and the characteristics of the interactions in succeeding generations. Enlargement of the time frame allows us to view these interactions relative to one another and arrive at causal mechanisms for parasite production in general. Factors pertaining to host preference such as frequency dependence and preimaginal conditioning may actually produce changes in system composition. These changes can occur in an evolutionary context altering the range of hosts available for attack through permanent shifts in preference. In the short-run, nonpermanent shifts in attack may be effected through frequency and conditioning.

In terms of managing MHP systems the above factors will determine the success or failure of the project. The relationship between one host (pest) and its parasite will be strengthened if frequency dependence and conditioning prove favorable. However, periods of low pest numbers can force parasites to preferentially attack nontarget hosts. Therefore, long-term relationships for MHP systems must be conceptualized and managed within this context.

SUMMARY AND CONCLUSIONS

Successful use of parasites in IPM programs requires that parasites must be researched as the object of control. In the past they have been viewed as uncontrollable management options with little appreciation for the complexity inherent in their ecology. This outlook has lead to a pesticidal approach to application and evaluation of parasites (i.e., controlling the amount being applied at application time and evaluating their performance in terms of percent kill). Therefore, resources in this classical context have been channeled toward those factors controlling pest numbers rather than parasite numbers.

Analysis of the ETC-FWW system showed that an expanded system conceptualization is a necessity for understanding the determinants of parasitism. Thus, the basic one-to-one parasite-host interaction is important, but host-host interactions may ultimately explain the majority of the variability in multiple host systems. Host-host interactions include those processes mediated through common parasites and through common host plants.

In addition to increasing the required number of system components, a reductionist approach is needed to understand their interactions. In the model developed in this study, results of sensitivity analyses of the varying phenotypic composition of FWW populations exemplified this need. In this case, parasite pressure applied to ETC in the subsequent generation was significantly affected by composition. In addition, this "micro" view suggests that attempting to characterize pest populations as a single number is not sufficient to evaluate a parasite's effectiveness on one or more hosts.

From an analytical perspective the increase in system complexity (within and between components) complicates the analysis of parasite systems. However, from a management perspective, many new control options are generated. For example, within a component, explicitly harvesting certain portions of a pest population provides managers with the ability to alter a population's susceptibility to parasitism. Thus, the probability of being parasitized becomes a controlled management option. Techniques involving population interaction are also possible with manipulations made on first generation hosts and parasites aimed at impacting second generation hosts.

Once the analysis of the ETC-FWW system was completed, a framework was produced to conceptualize various types of parasite systems. Basically, there were two major classes: single host and multiple host systems (SHP and MHP, respectively). These two types were further dichotomized into multiple generation single host systems, and synchronous (MHPS) and asynchronous multiple host systems (MHPA). For SHP systems, results of the analysis provided a model in which to view the various processes determining parasite production. Many of the factors identified in the model have been explored in field situations and deemed viable management techniques for one-to-one interactions. In terms of MHP systems, factors such as frequency dependance and pre-imaginal and imaginal conditioning will determine the success or failure of a program. Changes can occur in a MHP system altering the range of hosts available for attack in the long-run. In the short-run, non-permanent shifts in attack may be effected through frequency and conditioning.

Development of generalized system concepts for the management of parasites has provided a framework to examine specific techniques for pest management systems. Use of this framework insures that studies will be goal-oriented and resources directed through appropriate channels. By using a holistic philosophy along with the altered concept of parasites as the object of control, it is anticipated that parasites will become controllable variables and viable options in low energy IPM programs.

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APPENDIX A

SIMULATION MODEL OF THE ETC-FWW SYSTEM

```
      PROGRAM WORM (INPUT=65,OUTPUT=65,TAPE1=65,TAPE2=65,
     +TAPE3=65,TAPE4=65,TAPE5=65,TAPE6=65,TAPE7=65,TAPE8=65,TAPE9=65,
     +TAPE10=65,TAPE11=65,TAPE12=65)
      COMMON /DEBUG/ IFPRINT(10)
      COMMON /FOLK/ ECUMDD,CUMDD,PCUMDD,ETHOST,THOST,PARA,RNORM(8,10)
      COMMON /FOLK/ RKPTOT(10),R2PAR(8,10),R2KPTOT(10),R3ENC(8,10)
      COMMON /FOLK/ R3KPTOT(10),MINSTAR,TOWWEB,PARAP,PPCTKP(10)
      COMMON /FOLK/ EPCTKP(10),UNPARIN(8),PARIN(8),ENCIN(8)
      COMMON /FOLK/ UNPARKP(10),PARKP(10),ENCKP(10)
      COMMON/FOLK/STRG(10,10,3),PARHOST,ENCHOST,PTHOST
      COMMON/BILL/WTDMINE,WTDMINF
      REAL PRIN(10),PROUT(10),PR(10,10),ZSTRG(10),AM(3),A1(2)
      REAL PAMT(6),XKP(6),ROUT(9,10,3),P(10),DEL(10),DELP(10)
      REAL HOST(8),R(10,8,10),SURV(8),ESURV(7),PARACO(3),ENCAP(10)
      REAL PHOST(8),EHOST(8),DE(10),DEP(10),R3(10,8,10),OWWEB(10)
      REAL RA(100),RB(200),EKP(10),PLRN(8),R2(10,8,10)
      REAL A(10),B(10),STORE(10,8,10),STORE1(10,1,1),TOTKP(10)
      REAL PROUTI(10),ROUTI(8),TOM(10),PESTRG(7),ETSTRG(7),EDEL(7)
      REAL EDELP(7),E(7),F(7),PUPALWT(10),EGGS(10),PAR(10),PPAR(10)
      REAL ETOUTI(7),PEOUTI(7),TEOUTI(7),PHOSTI(8),EHOSTI(8),THOSTI(8)
      REAL OWPARA(10),IPAWS(10),PENCP(10),EENCP(10)
      REAL NEWX,NEWY,INSTAR(6),MINSTAR
      REAL XINS(6),PROPF(6)
C INITIALIZATION AND PARAMETERIZATION OF SOME VARIABLES
      DATA PARACO(1),PARACO(2),PARACO(3)/.3,.7,1.0/,
     +ENCAP(1),ENCAP(2),ENCAP(3),ENCAP(4),ENCAP(5),ENCAP(6),
     +ENCAP(7),ENCAP(8),ENCAP(9),ENCAP(10)/0.,0.,0.,1.66,1.5,1.0,
     +0.,0.,0.,0./,EKP(1),EKP(2),EKP(3),EKP(4),EKP(5),EKP(6),
     +EKP(7),EKP(8),EKP(9),EKP(10)/.6,.52,.42,.37,.29,.22,.15,.08,
     +0.,0./,K/10/,APLRN/0./
     +,A(1),A(2),A(3),A(4),A(5),A(6),A(7),A(8),A(9),A(10)/-0.228631,
     +-0.306721,-0.448932,-0.559971,-0.559971,-0.447777,-0.212374,
     +-0.340179,
     +-0.067198,-0.0239933/,B(1),B(2),B(3),B(4),B(5),B(6),B(7),B(8),B(9)
     +,B(10)/0.004482,0.006013,0.008802,0.010977,0.010977,0.008778
     +,0.004164,0.006669,0.001600,0.005713/
      DATA IFLAG1,IFLAG2/0,0/
      DATA STRG/300*0./
      DATA AM,A1/5*0./
      DATA ROUTI/8*0./
      DATA TOM/10*0./
      DATA RA,RB/300*0./
      DATA E/-.224351,-.472431,-.579370,-.763769,-.763769,-.763769,
     +-27.946828/
      DATA F/.004654,.009802,.012025,.015851,.015851,.015851,.550767/
      DATA PUPALWT/150.0,153.0,155.0,155.0,154.0,153.0,150.0,144.0,
     +139.0,128.0/
      DATA OWPARA/10*0./
      DATA IPAWS/10*0./
      DATA PROPF/.279,.208,.142,.114,.114,.143/
```

```
      DATA BASE1,BASE2,BASE3/51.,42.,48.2/
C
C **********************BEGIN SIMULATION**********************
C VARAIBLES INITIALIZED
C
      REWIND 1
      DT=0.1
      Q1=DT*24.
      HOUR= (22./7.)/24.
      TIME=0.
      N=1./DT+.5
      DO 1500 I=1,10
      READ*,PRIN(I)
      PRINT*,"PRIN",I,"=",PRIN(I)
      PRIN(I)=PRIN(I)/DT
      ZSTRG(I)=PRIN(I)
1500  CONTINUE
      PRINT*,"ENTER NDAYS TO RUN..."
      READ*,NDAYS
      PRINT*,"NDAYS=",NDAYS
      WRITE 60
60    FORMAT(1X,*ENTER PARASITE DENSITY*)
      READ 70,SUMPP
70    FORMAT(F10.2)
      PRINT*,SUMPP
      SUMPP=SUMPP/DT
      WRITE 80
80    FORMAT(1X,*ENTER EASTERN TENT CAT. DENSITY*)
      READ 70,ETCIN
      PRINT*,ETCIN
      ETCIN=ETCIN/DT
666   FORMAT (1X,*DEBUG TABLE, PRINT STEP (2I2)*)
1     READ 667,I,J
667   FORMAT (2I2)
      IF (I .LT. 1  .OR.  I .GT. 9) GO TO 2
      IFPRINT(I) = J
      GO TO 1
2     CONTINUE
      PRINT*,"ENTER HARVEST INTERVAL AND EFFICACY (SB,SE,EFF)..."
      READ*,SPRAYB,SPRAYE,EFFIC
      PRINT*,SPRAYB,SPRAYE,EFFIC
C
C-----------------------------------------------------------
C
C CALCULATION OF THE NUMBER OF EGGS LAID/FEMALE FOR EACH KP CLASS
      DO 111 I=1,10
      EGGS(I)=3.8*PUPALWT(I)-134.0
111   CONTINUE
C     SET VALUES FOR YEARS
      PAIN=0.
```

```
      TWPARA=0.
      DOUTI=0.
      PAOUTI=0.
      CUMDD=0.
      PCUMDD=0.
      ECUMDD=0.0
      PLRP=0.
      DO 1700 I=1,10
      PROUTI(I)=0.0
      OWWEB(I)=0.
      PROUTI(I)=0.
      PAR(I)=0.
      PENCP(I)=0.
      EENCP(I)=0.
      PPAR(I)=0.
      DO 1800 J=1,10
      PR(I,J)=0.
      DO 1900 JJ=1,8
      R(I,JJ,J)=0.
      R2(I,JJ,J)=0.
      R3(I,JJ,J)=0.
      STORE(I,JJ,J)=0.
      IF(I.GT.9)GO TO 1900
      IF(JJ.GT.3)GO TO 1900
      ROUT(I,J,JJ)=0.0
1900  CONTINUE
1800  CONTINUE
      IF(I.GT.8)GO TO 1700
      PHOSTI(I)=0.
      THOSTI(I)=0.
      EHOSTI(I)=0.
      RB(I)=0.
      PLRN(I)=0.
      IF(I.GT.6)GO TO 1700
      XKP(I)=0.
      IF(I.GT.4)GO TO 1700
      RA(I)=0.
      DO 1710 II=1,8
      DO 1720 J=1,10
      RNORM(II,J)=0.
      R2PAR(II,J)=0.
      R3ENC(II,J)=0.
1720  CONTINUE
1710  CONTINUE
1700  CONTINUE
      DO 123 I=1,10
      RKPTOT(I)=0.0
      R2KPTOT(I)=0.0
      R3KPTOT(I)=0.0
123   CONTINUE
```

```
C
C *********************THE 1400 LOOP IS THE DAILY LOOP***********
C
      DO 1400 KJ=1,NDAYS
      HTIME=0.
C READ FROM TAPE1--THE TEMPERATURE FILE
      READ(1,50)IDAY,TMIN,TMAX
50    FORMAT(13X,I3,32X,2(F8.2,2X))
C
C CALCULATE DEGREE-DAYS
      CALL  DEGDAY (TMAX,TMIN,BASE1,FRFDD)
      CALL DEGDAY (TMAX,TMIN,BASE2,FRPDD)
      CALL DEGDAY(TMAX,TMIN,BASE3,FREDD)
      HRANG=(TMAX-TMIN)/2.
      TMEAN=(TMAX+TMIN)/2.
C
C **********************THE 99 LOOP IS THE DT LOOP*************
C
      DO 99 MM=1,N
C
C ACCUMULATE DEGREE-DAYS AND CALCULATE INSTANTANEOUS TEMPS.
      CUMDD=CUMDD+FRFDD*DT
      PCUMDD=PCUMDD+FRPDD*DT
      ECUMDD=ECUMDD+FREDD*DT
      HTIME=HTIME+Q1
      THETA=(HTIME-9.)*HOUR
      TEMP=TMEAN+HRANG*SIN(THETA)
      TIME=TIME+DT
C
C-----------------------------------------------------------------
      CALL DELAY (TEMP,DEL,EDEL,A,B,E,F)
      IF(KJ.GT.1.OR.MM.GT.1)GO TO 6
      DO 2100 I=1,10
      DELP(I)=DEL(I)
      IF(I.GT.7) GO TO 2100
      EDELP(I)=EDEL(I)
2100  CONTINUE
      FLAG=1.
C-----------------------------------------------------------------
C
C CALCULATE SURVIVALS FOR ETC (ESURV) AND FWW (SURV)
6     CALL SURVIV(CUMDD,SPRAYB,SPRAYE,EFFIC,SURV,ESURV)
C
C-----------------------------------------------------------------
C
C PARASITE PUPAL AND ADULT DELAYS
C
      CALL DELLVF(PAIN,PAOUT,PAR,PARA,DEL(9),DELP(9),DT,K,STORE1(1,
     +1,1))
      CALL DELLVF(SUMPP,PAIN,PPAR,PARAP,DEL(10),DELP(10),DT,K,STORE
```

```
     +1(1,1,1))
      SUMPP=0.
      PAOUTI=PAOUTI+(PAOUT*DT)
C
C -----------------------------------------------------------------
C
C CALLING ETC SUBROUTINE TO CALCULATE DELAYS AND NEW SUMPP
C
      CALL EASTC(ETCIN,EDEL,EDELP,DT,ESURV,PARA,PARACO,SUMPP,
     +PESTRG,ETSTRG,FLAG,ETOUTI,PEOUTI,TEOUTI,TEMP,ETHOST,PTHOST)
C
C-------------------------------------------------------------------
      IF(ETOUTI(4).LT.2.) GO TO 968
C
C THE FOLLOWING IS USED IN THE COMPUTATION OF THE ADULT DELAYS
C
      IF ( ETSTRG(4) .GE. 1.0 ) GO TO 968
      IFLAG1 = IFLAG1 + 1
      IF ( IFLAG1 .EQ. 1 ) IETC = IDAY
968   DOUT=0.0
      SPUPAE=0.0
      DO 100 J=1,10
      BIGX=.01*PRIN(J)
      IF(ZSTRG(J).LE.BIGX)GO TO 100
      ABEL=(CUMDD-(280.+J*40.))/12.
      IF(ABEL.LT.-3.)GO TO 1713
      IF(ABEL.GE.3.)GO TO 1714
      XDENOM=0.
      IF(ABEL.GE.-.1.AND.ABEL.LT.0.0)ABEL=-.1
      IF(ABEL.GE.0.0.AND.ABEL.LT.0.1)ABEL=.1
      CALL ZSCORE(ABEL,BAK,EBAR)
      GO TO 1715
1713  BAK=0.
      GO TO 1715
1714  BAK=1.0
1715  DICK=BAK*PRIN(J)
      PROUT(J)=DICK-TOM(J)
      ZSTRG(J)=PRIN(J)-DICK
      TOM(J)=DICK
      SPUPAE=SPUPAE+ZSTRG(J)
      DOUT=DOUT+PROUT(J)
      PROUTI(J)=PROUTI(J)+(PROUT(J)*DT)
100   CONTINUE
      DOUTI=DOUTI+(DOUT*DT)
C ------------------------------------------------------------------
C
C -----------------------MATING MODEL---------------------------
C
      AM(1)=.65*DOUT
      A1(1)=.23*DOUT
```

```
      A1(2)=.12*DOUT
      CALL DCTDEL(A1(1),AM(2),RA,N)
      CALL DCTDEL(A1(2),AM(3),RB,N*2)
      TMATE=AM(1)+AM(2)+AM(3)
      DO 300 I=1,3
      IF(TMATE.EQ.0.)GO TO 300
      AM(I)=AM(I)/TMATE
300   CONTINUE
C-----------------------------------------------------------------
C
C PAMT(I) EQUALS THE DENSITY IN EACH MATING CLASS
      PAMT(1)=(AM(1)**2)*TMATE
      PAMT(2)=(AM(2)**2)*TMATE
      PAMT(3)=(AM(3)**2)*TMATE
      PAMT(4)=AM(1)*AM(2)*2*TMATE
      PAMT(5)=AM(1)*AM(3)*2.*TMATE
      PAMT(6)=AM(2)*AM(3)*2.*TMATE
C-----------------------------------------------------------------
C
C XKP(I) EQUALS THE MEAN KP OF THE OFFSPRING BETWEEN EACH MATING
C                            CLASS
      XKP(1)=EXP(2.456+0.602*ALOG(CUMDD))
      Z=CUMDD-20.
      IF(Z.LE.0.)GO TO 5
      XKP(2)=EXP(2.456+0.602*ALOG(CUMDD-20.))
      Z=CUMDD-40.
      IF(Z.LE.0.)GO TO 5
      XKP(3)=EXP(2.456+0.602*ALOG(CUMDD-40.))
      Z=(2.*CUMDD-20.)/2.
      IF(Z.LE.0.)GO TO 5
      XKP(4)=EXP(2.456+0.602*ALOG((CUMDD*2.-20.)/2.))
      Z=(2.*CUMDD-40.)/2.
      IF(Z.LE.0.)GO TO 5
      XKP(5)=EXP(2.456+0.602*ALOG((2.*CUMDD-40.)/2.))
      Z=(2.*CUMDD-60.)/2.
      IF(Z.LE.0.)GO TO 5
      XKP(6)=EXP(2.456+0.602*ALOG((2.*CUMDD-60.)/2.))
C-----------------------------------------------------------------
C
C CLEARING INPUT ARRAY FOR PREOVIPOSITIONAL ADULT DELAY
5     DO 400 I=1,10
      ROUT(9,I,1)=0.
400   CONTINUE
C-----------------------------------------------------------------
C
C CALCULATION OF STANDARD DEV. AND PLACEMENT OF EGGS INTO NEW CLASS
      DO 410 J=1,6
      IF(XKP(J).LE.330) GO TO 410
      SD=-1328.82+229.665*ALOG(XKP(J))
      NEWY=(300.-XKP(J))/SD
```

```
      CALL ZSCORE(NEWY,PY,EBAR)
      DO 420 I=1,10
      X=300.+(I*40.)
      NEWX=((X-XKP(J))/SD)
      IF(NEWX.LT.-3.0)GO TO 415
      IF(NEWX.GT.3.0)GO TO 414
      IF(NEWX.GE.-0.1.AND.NEWX.LT.0.0)  NEWX=-0.1
      IF(NEWX.GE.0.0.AND.NEWX.LT.+0.1) NEWX=+0.1
      CALL ZSCORE (NEWX,P(I),EBAR)
      GO TO 420
414   P(I)=1.0
      GO TO 420
415   P(I)=0.000001
420   CONTINUE
      ROUT(9,1,1)=P(1)*PAMT(1)+ROUT(9,1,1)
      IF(P(1).GE..98)GO TO 410
      DO 430 I=2,10
      IF(P(I).GE.0.99)GO TO 1299
      ROUT(9,I,1)=(P(I)-P(I-1))*PAMT(J)+ROUT(9,I,1)
      GO TO 430
1299  ROUT(9,I,1)=(1.-P(I-1))*PAMT(J)+ROUT(9,I,1)
      GO TO 410
430   CONTINUE
410   CONTINUE
C
C-------------------------------------------------------------------
C
C DELAYS FOR PREOVIPOSITIONAL ADULTS TO PUPAE
C
      DO 699 I = 1,8
      HOST(I)=0.
      PHOST(I)=0.
      EHOST (I) = 0.
      UNPARIN (I) = 0.
      PARIN (I) = 0.
      ENCIN (I) = 0.
699   CONTINUE
      DO 695 J = 1,10
      UNPARKP (J) = 0.
      PARKP (J) = 0.
      ENCKP (J) = 0.
695   CONTINUE
      DO 700 I=1,8
      II=I+1
      DO 800 J=1,10
      IF(I.LT.4.OR.I.GT.6) GO TO 444
C
C ATTRITION APPLIED TO NORMAL, PAR. AND ENCAP. FLOWS.
C
      DO 900 JJ=1,10
```

```
      ALOSS=PLRN(I)*R(JJ,I,J)
      R(JJ,I,J)=R(JJ,I,J)-ALOSS
      ELOSS=ALOSS*ENCAP(I)*EKP(J)
      R3(JJ,I,J)=R3(JJ,I,J)+ELOSS
      R2(JJ,I,J)=R2(JJ,I,J)+ALOSS-ELOSS
      RNORM(I,J)=RNORM(I,J)+R(JJ,I,J)
      R2PAR(I,J)=R2PAR(I,J)+R2(JJ,I,J)
      R3ENC(I,J)=R3ENC(I,J)+R3(JJ,I,J)
900   CONTINUE
444   DE(I)=DEL(I)
      DEP(I)=DELP(I)
C
C CALL DELAYS FOR ALL LIFE STAGES OF THE FWW
C
      CALL DELLVF(ROUT(II,J,1),ROUT(I,J,1),R(1,I,J),STRG(I,J,1),
     +DE(I),DEP(I),DT,K,STORE(1,I,J))
      ROUT (I,J,1)= ROUT (I,J,1) * SURV(I)
      ROUTI(I)=ROUTI(I)+(ROUT(I,J,1)*DT)
      IF(I.EQ.8) ROUT(I,J,1)=ROUT(I,J,1)*EGGS(J)/2.0
      IF(I.GT.6)GO TO 800
      DE(I)=DEL(I)
      DEP(I)=DELP(I)
      CALL DELLVF(ROUT(II,J,2),ROUT(I,J,2),R2(1,I,J),STRG(I,J,2),
     +DE(I),DEP(I),DT,K,STORE1(1,1,1))
      ROUT(I,J,2)=ROUT(I,J,2)*SURV(I)
      IF(I.LT.4)GO TO 800
      DE(I)=DEL(I)
      DEP(I)=DELP(I)
      CALL DELLVF(ROUT(II,J,3),ROUT(I,J,3),R3(1,I,J),STRG(I,J,3),
     +DE(I),DEP(I),DT,K,STORE1(1,1,1))
      ROUT(I,J,3)=ROUT(I,J,3)*SURV(I)
      IF(I.NE.4)GO TO 800
      ROUT(4,J,1)=ROUT(4,J,1)+ROUT(4,J,3)
      EENCP(J)=EENCP(J)+ROUT(4,J,3)*DT
800   CONTINUE
C
C INTEGRATES RATES FOR PAR., ENCAP. AND TOTAL WEBWORMS.
C
      PHOSTI(I)=PHOSTI(I)+PHOST(I)*DT
      EHOSTI(I)=EHOSTI(I)+EHOST(I)*DT
      THOSTI(I)=EHOSTI(I)+PHOSTI(I)
700   CONTINUE
      DO 2000 I=1,8
      DELP(I)=DEP(I)
2000  CONTINUE
C
C SUMMING ACROSS KP CLASSES FOR EACH LARVAL INSTAR.
      DO 33 I = 1,6
      DO 34 J=1,10
      UNPARIN (I) = UNPARIN (I) + STRG (I,J,1)
```

```
      PARIN (I) =   PARIN (I) + STRG (I,J,2)
      ENCIN (I) =   ENCIN (I) + STRG (I,J,3)
34    CONTINUE
      HOST  (I) =    HOST (I) + UNPARIN (I)
      PHOST  (I) =   PHOST (I) +   PARIN (I)
      EHOST  (I) =   EHOST (I) +   ENCIN (I)
33    CONTINUE
C SUMMING ACROSS LARVAL INSTARS FOR EACH KP CLASS.
      DO 35 J = 1,10
      DO 35 I = 1,6
      UNPARKP (J) = UNPARKP (J) + STRG (I,J,1)
      PARKP (J) =   PARKP (J) + STRG (I,J,2)
      ENCKP (J) =   ENCKP (J) + STRG (I,J,3)
35    CONTINUE
C SUMMING AVAILABLE HOSTS FOR PARASITISM
        THOST =  HOST(4) +  HOST(5) +  HOST(6)
C SUMMING PARASITIZED HOSTS
      PARHOST = PHOST(4) + PHOST(5) + PHOST(6)
C SUMMING ENCAPSULATED HOSTS
      ENCHOST = EHOST(4) + EHOST(5) + EHOST(6)
C SET UP FLAG TO COMPUTE IFWW TO BE USED IN CONNECTION WITH IDELAY
      IF ( HOST(6). LE . 1.0 ) GO TO 38
      IFLAG2 = IFLAG2 + 1
      IF ( IFLAG2.EQ.1 ) IFWW = IDAY
C----------------------------------------------------------
C CALLING ATTACK MODEL FOR THE FWW
38    CALL ATTACK(DT,THOST,PARA,PATT)
C--------------------------------------------------------------------
C REDUCES ATTACK RATE IN RESPONSE TO TEMPERATURES
C LESS THAN 65 AND GREATER THAN 90.  ATTACK IS REDUCED
C BY A LINEAR FUNCTION WITH A SLOPE OF .1 AT TEMPERATURES
C BETWEEN 60 AND 65.  ATTACK IS ALSO REDUCED BY A LINEAR
C FUNCTION AT TEMPERATURES BETWEEN 90 AND 110
C WITH A SLOPE OF .05.
C
      IF(TEMP.LE.60.)PATT=0.0
      IF(TEMP.GT.60..AND.TEMP.LE.65.)PATT=(TEMP-60.)*.2*PATT
      IF(TEMP.GT.90..AND.TEMP.LE.110.)PATT=(1.-.05*(TEMP-90.))*PATT
      IF(TEMP.GT.110.)PATT=0.
C--------------------------------------------------------------------
C
      DO 1000 I=1,3
      PLRN(I+3)=(PARACO(I)*PATT)
1000  CONTINUE
C
C----------------------------------------------------------------
C
C SUMMING OVERWINTERING NUMBERS
      TOWWEB=0.0
      DO 1100 J=1,10
```

```
C
C OUTPUT NOT INCLUDED IN SUBROUTINE DEBUG
      WRITE(11,137)IDAY,ECUMDD,(ETSTRG(JJ),JJ=1,7)
137   FORMAT(1X,I3,1X,8(E9.3,1X))
1400  CONTINUE
C-------------------------END DAILY LOOP (1400)----------------
C
C OUTPUTS FOR INITIALIZATION OF MULTIPLE YEAR RUNS
C
      PRINT*,"OW FWW PUPAE PER KP"
      PRINT 138,(OWWEB(JJ),JJ=1,10)
138   FORMAT(5X,10(E9.3,1X))
      DO 10 JKP=1,10
      WRITE(12,139)JKP,OWWEB(JKP)
139   FORMAT(I3,10(E9.3))
10    CONTINUE
      ENDFILE 12
      DO 11 JKP=1,10
      WRITE(12,139)JKP,OWPARA(JKP)
11    CONTINUE
      ENDFILE 12
C
      PRINT*,"ETC PUPAE"
      PRINT 138,ETOUTI(1)
C ETCEGG COMPUTED FROM 220 EGGS PER MASS AND SURVIVAL
C OF .47 AND .47 FOR PUPAL AND ADULT STAGES.
      ETCEGG=ETOUTI(1)*48.4*.5
      PRINT*,"ETC EGGS TO OVERWINTER"
      PRINT 138,ETCEGG
C
      PRINT*,"CAMPOPLEX FROM ETC"
      PRINT 138,PEOUTI(1)
      PRINT*,"OW PARASITES PER KP"
      PRINT 138,(OWPARA(JJ),JJ=1,10)
      PRINT*,"TOTAL OW PARASITES"
      PRINT 138,TWPARA
C
C COMPUTE DELAY = IFWW - IETC
      IDELAY = IFWW - IETC
      PRINT 39,IDELAY
39    FORMAT (5X, " DELAY IN DAYS = ",I4 )
      END
```

```
      OWWEB(J)=OWWEB(J)+ROUT(1,J,1)*DT
      TOWWEB=TOWWEB+OWWEB(J)
      OWPARA(J)=OWPARA(J)+ROUT(1,J,2)*DT
      TWPARA=TWPARA+ROUT(1,J,2)*DT
1100  CONTINUE
C ------------------------------------------------------
C
C THIS PORTION OF THE PROGRAM DETERMINES MEAN LARVAL INSTAR
      DO 79 I=1,6
      INSTAR(I)=HOST(I)+PHOST(I)
      IF(I.LE.3)GO TO 79
      INSTAR(I)=INSTAR(I)+EHOST(I)
79    CONTINUE
      XNUM=0.
      WINSTAR=0.
      TINSTAR=0.
      XDENOM=0.
      WTDMINF=0.
      MINSTAR=0.
      DO 81 I=1,6
      TINSTAR=TINSTAR+INSTAR(I)
      WINSTAR=WINSTAR+INSTAR(I)*(7-I)
      XINS(I)=INSTAR(I)
      XI=I
      XNUM=XNUM+(PROPF(I)*(7.-XI)*XINS(I))
      XDENOM=XDENOM+(PROPF(I)*XINS(I))
81    CONTINUE
      IF ( TINSTAR.EQ.0.0) GO TO 99
      IF(XDENOM.EQ.0.)GO TO 99
C COMPUTE MEAN LARVAL INSTAR
      MINSTAR=WINSTAR/TINSTAR
      WTDMINF=XNUM/XDENOM
99    CONTINUE
C -------------------------END OF DT LOOP (99)----------------
C
C DETERMINE _ PARASITIZED AND ENCAPSULATED FOR EACH KP CLASS.
      DO 36 J = 1,10
      TOTKP (J) = UNPARKP (J) + PARKP (J) + ENCKP (J)
      IF ( TOTKP (J).EQ.0.0 ) GO TO 37
      PPCTKP(J) =   PARKP (J) / TOTKP (J)
      EPCTKP(J) =   ENCKP (J) / TOTKP (J)
      GO TO 36
37    PPCTKP(J)=0.
      EPCTKP(J)=0.
36    CONTINUE
C
C SUBROUTINE DEBUG GENERATES OUTPUT TABLES
      DO 668 ITBL = 1,9
      CALL DEBUG (ITBL, IDAY)
668   CONTINUE
```

```
      SUBROUTINE EASTC (X,EDEL,EDELP,DT,ESURV,PARA,PARACO,
     +SUMPP,PESTRG,ETSTRG,FLAG,ETOUTI,PEOUTI,TEOUTI,TEMP,ETHOST,PTHOST)
      COMMON/BILL/WTDMINE,WTDMINF
      DIMENSION ETOUT(8),ETCR(12,7),ETSTRG(7),EDEL(7),EDELP(7),
     +ESTORE(12,7),ESURV(7),PEOUT(8),PETCR(12,7),PESTRG(7),
     +EDEL1(7),EDELP1(7),PSTORE(12,7),PARACO(3),ETOUTI(7)
     +,PEOUTI(7),TEOUTI(7)
      DIMENSION EINSTAR(6),PROPE(6)
      DATA PROPE/.3058,.1460,.1172,.0897,.0897,.0897/
      IF(FLAG.EQ.0.)GO TO 6
C ---------------------------------------------------
C INITIALIZING DELAY VARIABLES FOR FIRST OF YEAR
C
      DO 4 I=1,7
      ETOUTI(I)=0.
      PEOUTI(I)=0.
      ETOUT(I)=0.
      ETSTRG(I)=0.
      PEOUT(I)=0.
      PESTRG(I)=0.
      DO 5 J=1,12
      ETCR(J,I)=0.
      ESTORE(J,I)=0.
      PETCR(J,I)=0.
      PSTORE(J,I)=0.
5     CONTINUE
4     CONTINUE
      FLAG=0.
      PEOUT(8)=0.
C ------------------------------------------------------
C
C BEGINNING OF ETC DELAYS
C
6     K=12
      ETOUT(8)=X
      DO 1 I=1,7
      II=I+1
      EDEL1(I)=EDEL(I)
      EDELP1(I)=EDELP(I)
      CALL DELLVF(ETOUT(II),ETOUT(I),ETCR(1,I),ETSTRG(I),EDEL1(I),
     +EDELP1(I),DT,K,ESTORE(1,I))
      ETOUT(I)=ETOUT(I)*ESURV(I)
      ETOUTI(I)=ETOUTI(I)+ETOUT(I)*DT
7     IF(I.GT.6)GO TO 1
C
C DELAYS FOR PARASITIZED ETC
C
      CALL DELLVF(PEOUT(II),PEOUT(I),PETCR(1,I),PESTRG(I),EDEL(I),
     +EDELP(I),DT,K,PSTORE(1,I))
      PEOUT(I)=PEOUT(I)*ESURV(I)
```

```
      PEOUTI(I)=PEOUTI(I)+PEOUT(I)*DT
      TEOUTI(I)=PEOUTI(I)+ETOUTI(I)
1     CONTINUE
      EDELP(7)=EDELP1(7)
C
C SUMMING PARASITIZED HOSTS
      PTHOST=PESTRG(4)+PESTRG(5)+PESTRG(6)
C SUMMING HOSTS AVAILABLE FOR ATTACK
C
      ETHOST=ETSTRG(4)+ETSTRG(5)+ETSTRG(6)
      CALL ATTACK(DT,ETHOST,PARA,PATT)
C ---------------------------------------------------
C REDUCES ATTACK RATE IN RESPONSE TO TEMPERATURES
C LESS THAN 65 AND GREATER THAN 90.  ATTACK IS REDUCED
C BY A LINEAR FUNCTION WITH A SLOPE OF .1 AT TEMPERATURES
C BETWEEN 60 AND 65.  ATTACK IS ALSO REDUCED BY A LINEAR
C FUNCTION AT TEMPERATURES BETWEEN 90 AND 110
C WITH A SLOPE OF .05.
C*********************************************************************
      IF(TEMP.LE.60.)PATT=0.0
      IF(TEMP.GT.60..AND.TEMP.LE.65.)PATT=(TEMP-60.)*.2*PATT
      IF(TEMP.GT.90..AND.TEMP.LE.110.)PATT=(1.-.05*(TEMP-90.))*PATT
      IF(TEMP.GT.110.)PATT=0.
C*****************************************************************
C
C APPLICATION OF PARASITE ATTACK
C
      DO 2 I=4,6
      EPLRN=PARACO(I-3)*PATT
      DO 3 J=1,12
      ALOSS=EPLRN*ETCR(J,I)
      ETCR(J,I)=ETCR(J,I)-ALOSS
      PETCR(J,I)=PETCR(J,I)+ALOSS
3     CONTINUE
2     CONTINUE
      SUMPP=PEOUT(1)
      X=0.
      DO 99 I=1,6
      EINSTAR(I)=0.
99    CONTINUE
      XNUME=0.
      XDENOME=0.
      WTDMINE=0.
C CALCULATE WEIGHTED MEAN INSTAR FOR ETC.
      DO 100 I=1,6
      YI=I
      EINSTAR(I)=EINSTAR(I)+PESTRG(I)+ETSTRG(I)
      XNUME=XNUME+(PROPE(I)*(7.-YI)*EINSTAR(I))
      XDENOME=XDENOME+(PROPE(I)*EINSTAR(I))
100   CONTINUE
```

```
      IF(XDENOME.EQ.0.)RETURN
      WTDMINE=XNUME/XDENOME
      RETURN
      END
C
C---------------------------------------------------------------
C
      SUBROUTINE ZSCORE(X,P,D)
      AX=ABS(X)
      T=1.0/(1.0+.2316419*AX)
      D=0.3989423*EXP(-X*X/2.0)
      P=1.0-D*T*((((1.330274*T-1.821256)*T+1.781478)*T-0.3565638)*T+0.3
     +193815)
      IF(X)1,2,2
1     P=1.0-P
2     RETURN
      END
C---------------------------------------------------------------
C
      SUBROUTINE ATTACK(TAG,ANO,P,PATT)
C  HOLLING DISC EQUATION--NO. OF ATTACKS/PARASITE
      A=(.046*ANO)/(1.+.00046*ANO)
C  CALCULATE NO. OF ATTACKS FOR PARASITE POPULATION
      ANA=A*TAG*P
      IF(ANA.LE..1)GO TO 1
      IF(ANO.LE.0.1)GO TO 1
C  GRIFFITHS AND HOLLING COMPETITION SUBMODEL
      ANHA=ANO*(1.0-(1.0+ANA/(ANO*50.))**(-50))
      PATT=ANHA/ANO
      RETURN
1     PATT=0.
      RETURN
      END
C---------------------------------------------------------------
C
      SUBROUTINE DELLVF(VIN,VOUT,R,STRG,DEL,DELP,DT,K,STORE)
      DIMENSION R(K),STORE(K)
      FK=FLOAT(K)
      A=DT*FK/DEL
      V=VIN
      DELD=(DEL-DELP)/(DT*FK)
      DELP=DEL
      DO 1 I=1,K
      DR=R(I)
      R(I)=DR+A*(V-DR*(1.+DELD))
      V=DR
1     CONTINUE
      VOUT=R(K)
      STRG=0.
      DO 2 I=1,K
```

```
      STORE(I)=R(I)*DEL/FK
      STRG=STRG+STORE(I)
2     CONTINUE
      RETURN
      END
C
C--------------------------------------------------------------
C
      SUBROUTINE SURVIV(CDD,SB,SE,EFF,SURV,ESURV)
      DIMENSION SURV(8),ESURV(7)
C THE DATA FOR THIS SUBROUTINE WAS TAKEN FROM MORRIS(1967,5TH
C PAPER) AND ITO AND MIYASHITA,1968.
C
C SURVIVAL COEFICIENTS FOR FWW
C
C SURV(1) IS APPLIED TO THE 6TH INSTAR OUTPUT BUT CONTAINS
C TWO COMBINED MORTALITY FACTORS, THAT OF THE 6TH INSTAR AND THE
C OVERWINTERING PUPAE.
      SURV(1)=(.45+RANF(X)*.1)*(.4+RANF(X)*.1)
C
C SURV(2)-SURV(6) ARE THE SURVIVAL COEFICIENTS FOR LARVAL INSTARS
C 5 THRU 1 RESPECTIVELY. SURV(7) IS THE EGG SURVIVAL COEF.
C AND SURV(8) IS THE ADULT SURVIVAL COEFICIENT.
C************************************************************
      SURV(2)=.45+RANF(X)*.1
      SURV(3)=.60+RANF(X)*.1
      SURV(4)=.7+RANF(X)*.1
      SURV(5)=.75+RANF(X)*.1
      SURV(6)=.55+RANF(X)*.1
      SURV(7)=.85+RANF(X)*.1
      SURV(8)=.75+RANF(X)*.1
C************************************************************
C
C SURVIVAL COEFFICIENT FOR ETC
C DATA IS TAKEN FROM RAVLIN UNPUBLISHED DATA 1980.
C ESURV(1)-(7) ARE COEFFICIENTS FOR EGGS THROUGH INSTAR 6.
C
C************************************************************
      ESURV(1)=.47+RANF(X)*.1
      ESURV(2)=.47+RANF(X)*.1
      ESURV(3)=.49+RANF(X)*.1
      ESURV(4)=.77+RANF(X)*.1
      ESURV(5)=.90+RANF(X)*.1
      ESURV(6)=.94+RANF(X)*.1
      ESURV(7)=.84+RANF(X)*.1
C************************************************************
      IF(CDD.LE.SB)GO TO 2
      IF(CDD.GT.SE)GO TO 2
      DO 1 IS=1,7
      SURV(IS)=SURV(IS)*EFF
```

```
1     CONTINUE
2     RETURN
      END
C
C-----------------------------------------------------------
C
      SUBROUTINE DEGDAY(XMAX,XMIN,BASE,XHEAT)
      DATA TPIE/6.283181/, HPIE/1.570795/
      IF(XMAX.GT.BASE) GO TO 1
      XHEAT=0.00001
      RETURN
C
C IF MAXIMUM TEMP GREATER THAN BASE ENTER HERE
C
1     Z=XMAX-XMIN
      XM=XMAX+XMIN
      IF(XMIN.LT.BASE) GO TO 2
      XHEAT=XM/2.-BASE
C
C ROUNDOFF- ODD UP--EVEN DOWN
C
      IF(XHEAT.GT.0.)GO TO 3
      XHEAT=.0001
3     RETURN
C
C IF MINIMUM TEMP LESS THAN BASE ENTER HERE
C
2     TBASE=BASE*2.
      A=ASIN((TBASE-XM)/Z)
      XHEAT=(Z*COS(A)-(TBASE-XM)*(HPIE-A))/TPIE
C
      IF(XHEAT.GT.0)GO TO 4
      XHEAT=.00001
4     RETURN
      END
C
C-------------------------------------------------------------
C
      SUBROUTINE DCTDEL(VIN,VOUT,VINT,N)
      DIMENSION VINT(N)
      VOUT=VINT(1)
      DO 1 I=2,N
1     VINT(I-1)=VINT(I)
      VINT(N)=VIN
      RETURN
      END
```

```
C----------------------------------------------------------------
C
      SUBROUTINE  DELAY  (TEMP,DEL,EDEL,A,B,E,F)
      DIMENSION  DEL(10),A(10),B(10),
     +EDEL(7),E(7),F(7)
C         CALCULATE  DEVELOPMENTAL  DELAYS FOR  WEBWORM.
      DO  10 I=1,8
      IF ( TEMP.LE.55.)  DEL(I)=100.
      IF  (TEMP.GT.55.)  DEL(I)=1./(A(I)+B(I)*TEMP)
10    CONTINUE
C
C        CALCULATE  DEVELOPMENTAL DELAYS FOR THE PARASITE.
      DO  20 K=9,10
      IF  (TEMP.LE.45.)  DEL(K)=700.
      IF  (TEMP.GT.45.)   DEL(K)=1./(A(K)+B(K)*TEMP )
20    CONTINUE
C DELAY FOR ETC EGGS
      IF(TEMP.LE.52.)EDEL(7)=100.
      IF(TEMP.GT.52.)EDEL(7)=TEMP/(E(7)+F(7)*TEMP)
C DELAYS FOR ETC L1-L6.
      DO 25 L=1,6
      IF(TEMP.LE.52.)EDEL(L)=100.
      IF(TEMP.GT.52.)EDEL(L)=1./(E(L)+F(L)*TEMP)
25    CONTINUE
      RETURN
      END
C
C----------------------------------------------------------------
C
      SUBROUTINE DEBUG (ITBL, IDAY)

C     PRINT STEP -IDAY- OF TABLE -ITBL-.

      COMMON /DEBUG/ IFPRINT(10)
      COMMON /FOLK/ ECUMDD,CUMDD,PCUMDD,ETHOST,THOST,PARA,RNORM(8,10)
      COMMON /FOLK/ RKPTOT(10),R2PAR(8,10),R2KPTOT(10),R3ENC(8,10)
      COMMON /FOLK/ R3KPTOT(10),MINSTAR,TOWWEB,PARAP,PPCTKP(10)
      COMMON /FOLK/ EPCTKP(10),UNPARIN(8),PARIN(8),ENCIN(8)
      COMMON /FOLK/ UNPARKP(10),PARKP(10),ENCKP(10)
      COMMON/FOLK/STRG(10,10,3),PARHOST,ENCHOST,PTHOST
      COMMON/BILL/WTDMINE,WTDMINF
      REAL MINSTAR

C     DETERMINE WHETHER TO PRINT STEP -IDAY- OF TABLE -ITBL-.
C     WE DON-T PRINT THE TABLE AT ALL UNLESS SPECIFICLY REQUESTED,
C     IF IFPRINT .GT. 0

      IF (IFPRINT(ITBL) .LE. 0) RETURN

C     IF EVERY STEP OF THE TABLE IS REQUESTED, WE DO PRINT.
```

```
      WRITE(4,88)
      RETURN
C                TABLE 4
400   WRITE(4,91)IDAY,CUMDD,PCUMDD
91    FORMAT(*0*,9X,*IDAY=*,I3,2X,*CUMDD=*,F9.3,4X,
     +*PCUMDD=*,F9.3,/,9X,*TABLE 4*,11X,*FWW-ENCAPSULATED*
     +* INDIVIDUALS*,/,9X,67(*-*),/,9X,*KP*,4X,*1*,9X,*2*,9X,
     +*3*,9X,*4*,9X,*5*,9X,*6*,5X,*TOTAL*,/,9X,67(*-*))
      DO 115 IK=1,10
      WRITE(4,90)IK,STRG(6,IK,3),STRG(5,IK,3),STRG(4,IK,3)
     +,STRG(3,IK,3),STRG(2,IK,3),STRG(1,IK,3),ENCKP(IK)
115   CONTINUE
      WRITE(4,88)
      WRITE(4,87)ENCIN(6),ENCIN(5),ENCIN(4),ENCIN(3),ENCIN(2)
     +,ENCIN(1)
      WRITE(4,88)
88    FORMAT(9X,67(*-*))
      RETURN


500   IF(IDAY.EQ.91)WRITE(5,996)
996   FORMAT(*1*,3X,*TABLE 5*,/,1X,*IDAY*,5X,*ECUMDD*,5X,
     +*WTDMINE*,4X,*CUMDD*,6X,*WTDMINF*,2X,*MINSTAR*,/,1X,65(*-*))
      WRITE(5,105)IDAY,ECUMDD,WTDMINE,CUMDD,WTDMINF,MINSTAR
105   FORMAT(1X,I3,3X,5(E9.3,2X))
      RETURN
C
C
600   IF(IDAY.EQ.91)WRITE(6,997)
997   FORMAT(*1*,10X,*T A B L E  6*,/,1X,*IDAY  CUMDD*,
     +6X,*PCUMDD*,5X,*TOWWEB*,5X,*PARAP*,/,1X,50(*-*))
      WRITE(6,106)IDAY,CUMDD,PCUMDD,TOWWEB,PARAP
106   FORMAT(1X,I3,4X,4(E9.3,2X))
      RETURN
C
C
700   IF(IDAY.EQ.91)WRITE(7,998)
998   FORMAT(*1*,41X,*T A B L E  7*,/,28X,10(*PCTPARA/*,2X),
     +/,1X,*IDAY  CUMDD*,6X,*PCUMDD*,7X,*KP 1*,5X,*KP 2*,5X,
     +*KP 3*,5X,*KP 4*,5X,*KP 5*,5X,*KP 6*,5X,*KP 7*,5X,*KP 8*,
     +5X,*KP 9*,5X,*KP 10*,/,1X,128(*-*))
      WRITE(7,109)IDAY,CUMDD,PCUMDD,(PPCTKP(J),J=1,10)
      RETURN
C
C
800   IF(IDAY.EQ.91)WRITE(8,999)
999   FORMAT(*1*,41X,*T A B L E  8*,/,28X,10(*PCTENCP/*,2X),
     +/,1X,*IDAY  CUMDD*,6X,*PCUMDD*,7X,*KP 1*,5X,*KP 2*,5X,
     +*KP 3*,5X,*KP 4*,5X,*KP 5*,5X,*KP 6*,5X,*KP 7*,5X,*KP 8*,
     +5X,*KP 9*,5X,*KP 10*,/,1X,128(*-*))
```

```
      IF (IFPRINT(ITBL) .EQ. 1) GO TO 10

C     PRINT IF MUDULUS SHOWS CORRECT STEP NUMBER.

      IF (MOD(IDAY,IFPRINT(ITBL)) .NE. 1) RETURN

C     BRANCH ON TABLE NUMBER TO CORRECT SET OF PRINTS.

10    GO TO (100,200,300,400,500,600,700,800)ITBL
C                  T A B L E  1
100   IF (IDAY .EQ. 91) WRITE (3,83)
83    FORMAT(*1*,7X,*TABLE 1*,24X,*TOTAL NUMBER OF HOSTS PER*,
     +* DAY*,/,7X,105(*-*),/,7X,*IDAY  ECUMDD    CUMDD*
     +*     PCUMDD    NORMETC    PARETC    NORMFWW   PARFWW*
     +*    ENCFWW    CAMPOPLEX*,/,7X,105(*-*))
      WRITE(3,85)IDAY,ECUMDD,CUMDD,PCUMDD,ETHOST,PTHOST,THOST
     +,PARHOST,ENCHOST,PARA
85    FORMAT(7X,I3,3X,9(E9.3,1X))
      RETURN
C                  T A B L E  2
200   WRITE (4,86) IDAY,CUMDD,PCUMDD
86    FORMAT(*1*,9X,*IDAY=*,I3,2X,*CUMDD=*,F9.3,4X,
     +*PCUMDD=*,F9.3,/,9X,*TABLE 2*,11X,*FWW-UNPARASITIZED*
     +* INDIVIDUALS*,/,9X,67(*-*),/,9X,*KP*,4X,*1*,9X,*2*,9X,
     +*3*,9X,*4*,9X,*5*,9X,*6*,5X,*TOTAL*,/,9X,67(*-*))
      DO 113 IK=1,10
      WRITE(4,90)IK,STRG(6,IK,1),STRG(5,IK,1),STRG(4,IK,1),STRG(3,IK,1)
     +,STRG(2,IK,1),STRG(1,IK,1),UNPARKP(IK)
90    FORMAT(9X,I2,1X,7(E9.3,1X))
113   CONTINUE
      WRITE(4,88)
      WRITE(4,87)UNPARIN(6),UNPARIN(5),UNPARIN(4),UNPARIN(3)
     +,UNPARIN(2),UNPARIN(1)
87    FORMAT(12X,6(E9.3,1X))
      WRITE(4,88)
      RETURN
C                  T A B L E  3
300   WRITE(4,89)IDAY,CUMDD,PCUMDD
89    FORMAT(*0*,9X,*IDAY=*,I3,2X,*CUMDD=*,F9.3,4X,
     +*PCUMDD=*,F9.3,/,9X,*TABLE 3*,11X,*FWW-PARASITIZED*
     +* INDIVIDUALS*,/,9X,67(*-*),/,9X,*KP*,4X,*1*,9X,*2*,9X,
     +*3*,9X,*4*,9X,*5*,9X,*6*,5X,*TOTAL*,/,9X,67(*-*))
      DO 114 IK=1,10
      WRITE(4,90)IK,STRG(6,IK,2),STRG(5,IK,2),STRG(4,IK,2)
     +,STRG(3,IK,2),STRG(2,IK,2),STRG(1,IK,2),PARKP(IK)
114   CONTINUE
      WRITE(4,88)
      WRITE(4,87)PARIN(6),PARIN(5),PARIN(4),PARIN(3),PARIN(2)
     +,PARIN(1)
```

```
      WRITE(8,109)IDAY,CUMDD,PCUMDD,(EPCTKP(J),J=1,10)
109   FORMAT(1X,I3,2X,2(E9.3,2X),10(F8.4,2X))
      RETURN
      END
```

APPENDIX B

DEGREE-DAY ACCUMULATIONS FOR GULL LAKE

1977-1979

1977 DEGREE-DAYS (> 9 C)

DAY	MARCH	APRIL	MAY	JUNE	JULY	AUG	SEPT
1	1	45	190	520	818	1284	1654
2	1	49	195	525	828	1295	1667
3	1	52	201	530	840	1309	1677
4	1	53	206	541	858	1325	1689
5	1	53	217	555	876	1340	1704
6	1	53	227	563	895	1354	1715
7	1	54	234	566	913	1368	1726
8	2	54	238	570	929	1381	1738
9	4	55	240	574	943	1393	1750
10	7	61	243	580	956	1407	1761
11	12	66	248	586	969	1420	1768
12	18	75	255	593	985	1429	1776
13	20	83	266	599	999	1440	1782
14	20	88	276	609	1013	1452	1788
15	24	95	287	618	1033	1461	1795
16	26	103	299	631	1052	1474	1803
17	26	113	313	647	1069	1483	1813
18	26	125	326	662	1084	1490	1826
19	26	136	341	674	1104	1497	1838
20	26	147	356	684	1124	1504	1844
21	26	157	372	692	1143	1511	1848
22	26	162	387	702	1156	1521	1856
23	26	164	402	713	1169	1531	1864
24	26	166	418	728	1182	1548	1874
25	26	166	433	742	1196	1555	1884
26	27	168	447	754	1206	1566	1893
27	30	173	458	768	1214	1582	1899
28	35	178	472	781	1226	1599	1907
29	39	181	485	794	1240	1612	1911
30	43	185	496	805	1254	1623	1917
31	45		509		1270	1638	

1977 DEGREE-DAYS (>11 C)

DAY	MARCH	APRIL	MAY	JUNE	JULY	AUG	SEPT
1	0	32	149	436	691	1109	1432
2	0	35	153	439	700	1119	1444
3	0	37	157	444	710	1131	1452
4	0	37	162	453	727	1146	1463
5	0	37	171	466	743	1159	1476
6	0	37	180	472	760	1171	1485
7	0	37	185	474	777	1184	1495
8	1	37	188	477	791	1196	1505
9	2	38	189	480	804	1206	1516
10	4	43	192	485	815	1219	1525
11	8	48	196	490	826	1229	1530
12	13	55	201	496	841	1237	1537
13	14	62	211	500	854	1246	1542
14	14	65	220	508	866	1257	1546
15	17	71	229	516	885	1265	1552
16	18	77	240	527	902	1276	1558
17	18	86	252	542	917	1284	1567
18	18	96	264	555	931	1289	1578
19	18	106	277	565	950	1295	1589
20	18	115	290	574	968	1300	1593
21	18	124	305	581	985	1306	1596
22	18	127	319	589	996	1314	1603
23	18	128	332	599	1008	1323	1608
24	18	130	346	612	1019	1338	1617
25	18	130	360	625	1032	1344	1626
26	19	131	373	635	1040	1354	1633
27	21	135	382	647	1048	1368	1638
28	24	140	394	659	1058	1384	1643
29	27	141	405	670	1070	1395	1647
30	30	144	415	680	1082	1404	1652
31	31		427		1097	1418	

1978 DEGREE-DAYS (> 9 C)

DAY	MARCH	APRIL	MAY	JUNE	JULY	AUG	SEPT
1	0	6	65	299	621	1008	1410
2	0	8	66	311	630	1021	1423
3	0	11	69	318	640	1034	1438
4	0	14	72	325	651	1043	1447
5	0	15	72	332	662	1051	1460
6	0	16	75	343	677	1061	1474
7	0	19	78	357	692	1074	1489
8	0	20	83	365	707	1088	1506
9	0	20	87	372	718	1099	1523
10	0	23	92	382	727	1111	1539
11	0	26	97	394	734	1123	1556
12	0	28	105	407	742	1136	1568
13	0	29	113	413	755	1151	1574
14	0	30	118	417	767	1167	1585
15	0	30	120	426	781	1185	1594
16	0	30	126	435	791	1201	1604
17	0	32	132	450	802	1215	1616
18	0	33	140	463	816	1230	1628
19	0	34	151	473	833	1246	1642
20	0	35	163	485	851	1255	1658
21	0	36	166	497	868	1265	1670
22	0	38	172	505	886	1277	1674
23	0	39	180	514	900	1293	1679
24	0	43	189	526	911	1309	1686
25	0	45	200	540	925	1324	1691
26	0	49	213	553	942	1337	1696
27	0	52	227	568	956	1351	1703
28	0	56	242	582	965	1366	1706
29	0	60	257	595	978	1378	1711
30	0	64	273	608	986	1390	1716
31	4		285		995	1400	

1978 DEGREE-DAYS (>11 C)

DAY	MARCH	APRIL	MAY	JUNE	JULY	AUG	SEPT
1	0	5	45	239	518	857	1212
2	0	6	46	250	525	868	1223
3	0	8	48	255	534	880	1237
4	0	10	50	261	543	887	1244
5	0	11	50	267	553	894	1255
6	0	12	52	276	566	903	1268
7	0	13	54	289	580	914	1281
8	0	14	58	296	592	926	1296
9	0	14	61	301	603	936	1312
10	0	16	64	309	610	947	1327
11	0	18	68	320	615	957	1342
12	0	20	74	332	622	969	1353
13	0	21	81	337	634	982	1357
14	0	21	84	340	644	996	1366
15	0	21	85	348	656	1012	1374
16	0	21	89	355	665	1027	1383
17	0	22	94	368	675	1039	1393
18	0	22	101	380	687	1053	1403
19	0	23	111	388	702	1068	1415
20	0	23	120	398	719	1075	1430
21	0	23	123	409	735	1083	1440
22	0	25	127	416	750	1094	1444
23	0	26	134	423	763	1108	1448
24	0	28	142	433	773	1122	1453
25	0	30	151	446	785	1136	1457
26	0	33	162	457	800	1148	1461
27	0	35	175	471	813	1160	1467
28	0	38	188	483	820	1173	1469
29	0	42	202	495	831	1184	1473
30	0	44	217	506	838	1194	1476
31	3		227		846	1203	

1979 DEGREE-DAYS (> 9 C)

DAY	MARCH	APRIL	MAY	JUNE	JULY	AUG	SEPT
1	0	27	89	285	605	1008	1363
2	0	27	95	292	616	1022	1378
3	0	27	101	301	626	1035	1393
4	0	27	102	312	636	1050	1406
5	0	27	103	323	643	1063	1419
6	0	27	109	336	651	1076	1432
7	0	27	119	350	660	1092	1446
8	0	27	132	365	672	1109	1456
9	0	27	145	380	687	1121	1460
10	0	27	159	392	699	1137	1465
11	0	27	170	399	714	1145	1477
12	0	33	173	405	730	1152	1488
13	0	40	176	413	746	1161	1500
14	0	41	180	425	762	1168	1514
15	0	41	184	439	779	1173	1523
16	0	42	188	453	792	1179	1528
17	1	43	193	467	805	1188	1535
18	6	45	205	476	814	1197	1544
19	8	48	216	486	824	1208	1554
20	9	53	222	499	835	1219	1560
21	10	59	228	512	847	1231	1566
22	14	64	231	525	861	1242	1575
23	20	69	237	531	876	1256	1580
24	22	77	240	537	891	1270	1584
25	22	82	244	543	907	1279	1590
26	22	86	247	551	919	1288	1598
27	22	87	251	564	933	1299	1607
28	22	88	254	575	949	1311	1616
29	23	88	261	589	964	1322	1625
30	26	88	269	598	979	1336	1636
31	27		276		995	1350	

1979 DEGREE-DAYS (>11 C)

DAY	MARCH	APRIL	MAY	JUNE	JULY	AUG	SEPT
1	0	18	65	224	500	856	1164
2	0	18	69	230	509	868	1177
3	0	18	74	238	518	879	1190
4	0	18	75	246	526	892	1202
5	0	18	75	257	532	904	1214
6	0	18	80	267	539	916	1225
7	0	18	88	280	546	930	1238
8	0	18	99	293	556	945	1246
9	0	18	110	307	570	956	1249
10	0	18	123	317	581	970	1253
11	0	18	133	323	594	977	1263
12	0	23	135	328	608	983	1273
13	0	29	137	334	623	990	1283
14	0	29	140	344	637	996	1296
15	0	29	143	357	652	1000	1303
16	0	29	146	370	664	1005	1307
17	0	30	150	382	676	1012	1313
18	4	32	160	389	683	1020	1320
19	5	34	169	398	692	1029	1329
20	6	37	175	409	701	1039	1333
21	6	42	180	421	712	1049	1338
22	10	46	182	432	723	1059	1346
23	15	51	187	437	737	1071	1350
24	15	57	189	442	751	1083	1353
25	15	60	191	447	765	1091	1359
26	15	63	194	454	775	1099	1365
27	15	64	196	465	788	1107	1372
28	15	64	199	475	803	1118	1380
29	16	64	204	487	816	1128	1388
30	17	64	211	494	829	1140	1398
31	18		216		844	1152	

APPENDIX C

DETERMINATION OF DEVELOPMENTAL TEMPERATURE THRESHOLD FOR ETC EGGS

DETERMINATION OF DEVELOPMENTAL TEMPERATURE THRESHOLD FOR ETC EGGS

Because the egg stage in the ETC is of importance in initializing sampling programs, extensive rearings were done on this life-stage. Ten egg masses were placed in each of six temperatures ranging from 45° F (7.22° C) to 95° F (35.29° C). Each egg mass was monitored daily with the number of individuals emerging recorded.

Development was recorded in terms of the number of days required to hatch as a function of temperature (Fig. C.1A). After tabulating these values, each is inverted so as to transform them to percent development per day. Threshold determination is done by regressing percent/day on temperature and calculating the point at which there is 0% development/day. This analysis was performed on the linear portion of the data with 10.26° C calculated as the base temperature (Fig. C.1B). This number represents only an initial estimate for the second portion of the analysis.

The standard error technique (Casagrande 1971) was used in lieu of possible nonlinearity. Here, T_o's bracketing the suspected true base (as estimated through regression) are used in calculating degree-day accumulations. Standard errors are calculated for each assumed base over the range of rearing temperatures. The point at which the standard error is minimized provides the best fit for the given data set $T_o = 9°$ C (Fig. C.1C).

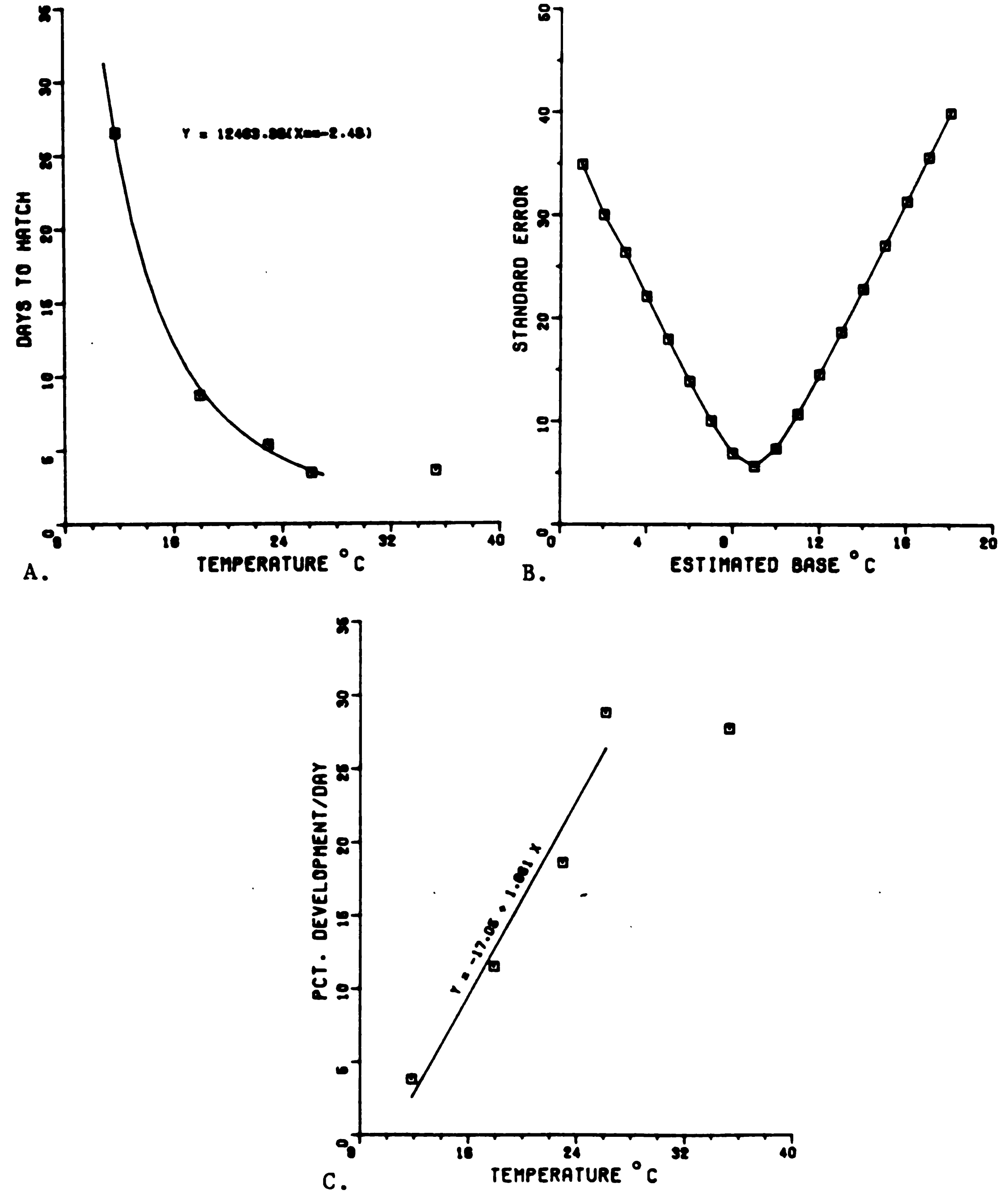
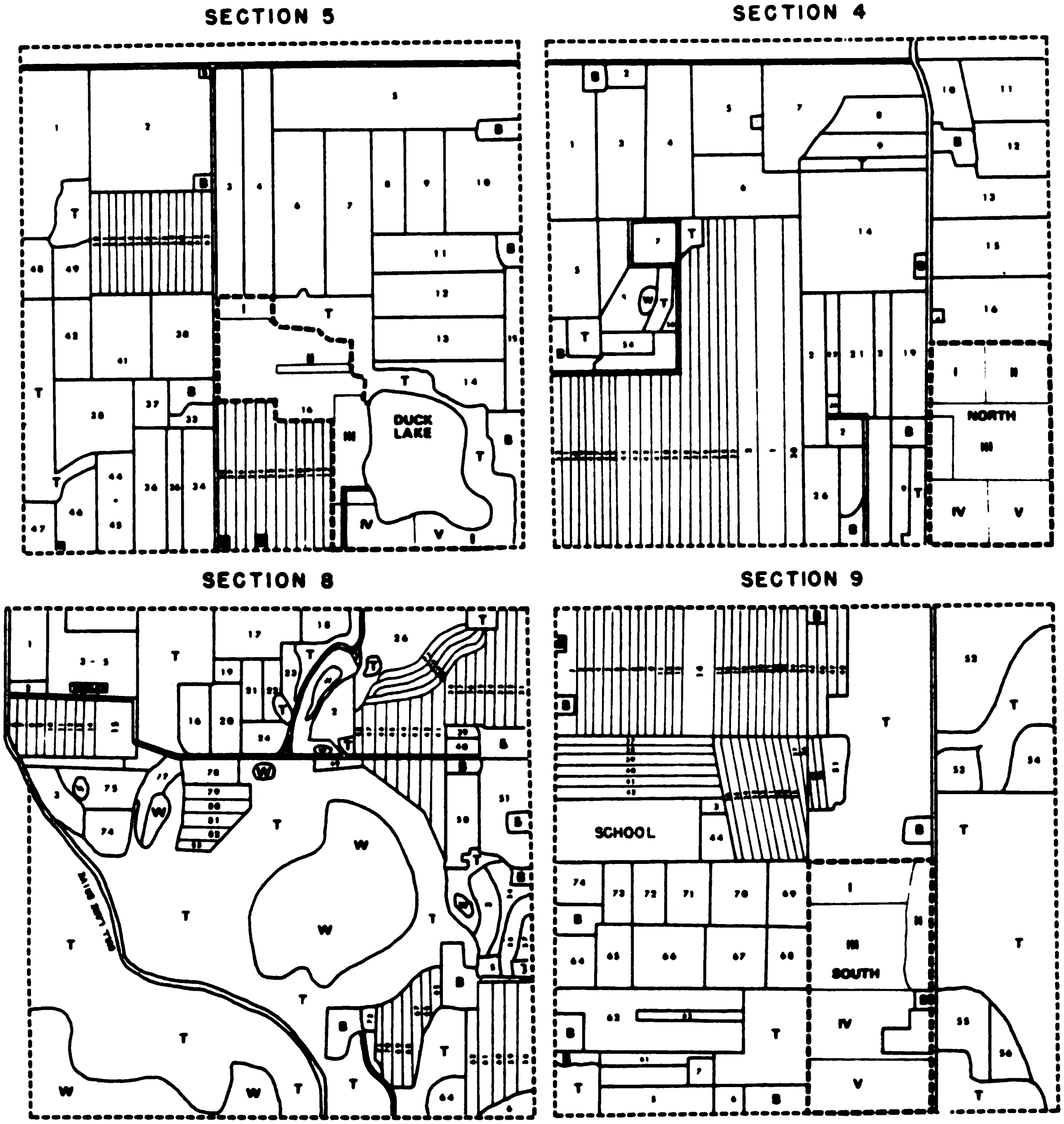


Figure C.1. Time-temperature functions and determination of T_o for ETC eggs.

APPENDIX D

STUDY AREAS AT THE KELLOGG BIOLOGICAL STATION



Study areas within the KBS.

APPENDIX E

POPULATION ESTIMATORS FOR PARASITES AND COLONIAL HOSTS

POPULATION ESTIMATORS FOR PARASITES AND COLONIAL HOSTS

Before undertaking any sampling program there is a need to identify the population parameters required as dictated by the project objectives and characteristics of the sample units. As alluded to above, the objectives are to examine parasitism rates and production of adult parasites throughout the course of a growing season. These rates and numbers will then be related back to the size of the host population, its age, and any other parameters of interest.

The need to provide probablistic statements concerning population size is characteristic of many host-parasite studies. This need, in most instances, is adhered to only with reference to the host population. Parasitism is typically viewed as a mean value (percent) with no reference to the precision of that point estimate. The following treatment serves to present estimators for both host and parasite populations and methods for reducing variance terms.

HOST POPULATION ESTIMATORS

Because of the highly visible characteristic of both the ETC and FWW we have the ability to make very precise counts of the number of colonies per unit area. With reference to the total population the problem concerns estimating the number of larvae per colony. In order to accomplish this, whole colony samples were taken for each sample period and the total number of individuals determined. The mean number of larvae per colony ($\bar{y}$) is:

$$\bar{y} = \frac{1}{n_c} \sum_{i=1}^{n_c} y_i \qquad [1]$$

where:

y_i = the number of larvae in the ith colony, and

n_c = the number of colonies sampled.

The association variance term is:

$$s_c^{\,2} = \frac{1}{n_c - 1} \sum_{i=1}^{n_c} (y_i - \bar{y})^2. \qquad [2]$$

Because of the knowledge of the actual number of colonies, (N_c), the variance of the mean ($\bar{y}$) can be reduced with a "finite population correction" (FPC) or:

$$\mathrm{v\hat{a}r}(\bar{y}) = \left(\frac{N_c - n_c}{N_c}\right)\left(\frac{S_c^{\,2}}{n_c}\right) \qquad [3]$$

The FPC weights the variance term by the proportion of the population sampled ($N_c - n_c/N_c$).

Estimates arrived at, at the colony level, can now be projected to the entire host population (i.e., the total number of host larvae ($\hat{y}$)) with:

$$\begin{aligned} \hat{y} &= N_c\left(\frac{1}{n_c} \sum_{i=1}^{n} y_i\right) \\ &= \left(\frac{N_c}{n_c}\right) \sum_{i=1}^{n_c} y_i \qquad [4] \end{aligned}$$

The variance of $\hat{y}$ is:

$$\begin{aligned} \mathrm{var}(y) &= N_c\ (\mathrm{vary}(\bar{y})) \\ &= N_c \left(\frac{S_c^{\,2}(N_c - n_c)}{n_c}\right) \qquad [5] \end{aligned}$$

It should be noted once again that there is only a single component in var ($\hat{y}$) because of the knowledge of absolute colony density.

PARASITISM ESTIMATORS

Parasite studies in general dictate that host individuals fall principally into two classes, parasitized and unparasitized. In some instances a third class must be recognized, that being parasite eggs or larvae which have been encapsulated. This problem reduces to estimating the proportion of the host population parasitized and the proportion of parasite attacks which have been nullified by encapsulation. I will first derive the equations necessary for estimates at the colony level and further calculations necessary in the plot/subplot design. Within this context, a given number of colonies are sampled in each of the subplots pictured in Appendix D. This produces a 2-phase scheme. Phase 1 provides estimates of colony size, colony density, and total larval numbers (described above). Phase 2 includes samples taken from intact colonies and estimates of parasitism rates calculated.

The total number of attacks over a given time period is, of course, of great interest in our study of host-parasite relations. This includes both those individuals that have viable parasites and those containing encapsulated eggs and larvae. Let:

a_1 = the number of unparasitized hosts in the sample/colony,

a_2 = parasitized hosts, and

a_3 = the number of hosts containing encapsulated parasites.

Therefore, the proportion of the hosts attacked (P_a) is:

$$P_a = \frac{a_2+a_3}{a_1+a_2+a_3} \qquad [6]$$

The variance of P_a is:

$$S^2_{p_a} = \frac{n_1 p_a q_a}{n-1} \qquad [7]$$

As was done earlier (Eq. 3) the FPC is used to reduce $S^2_{p_a}$ or:

$$\text{var}(p_a) = \frac{N_1(N_1-n_1)}{n\ -1} p_a q_a \qquad [8]$$

with:

$$q_a = 1-p_a.$$

In this instance, an estimate of the number of larvae per colony (N_1) or $\bar{y}$ (Eq. 1) must be used in place of the absolute numbers in equation 3. Hence:

$$\text{var}(p_a) = \frac{\bar{y}(\bar{y}-n_1)}{n_1-1} p_a q_a \qquad [9]$$

where:

$$n_1 = a_1+a_2+a_3$$

= the number of larvae sampled in the colony.

In addition to the attack rate (p_a) the number of attacks producing viable parasites (p_p) (i.e., those escaping encapsulation) is calculated. The proportion of the colony being effectively parasitized is:

$$p_p = \frac{a_2}{a_1+a_2+a_3} \qquad [10]$$

Like equation 9 the variance of p_p is:

$$\text{var}(p_p) = \frac{\bar{y}(\bar{y}-n_1)}{n_1-1} p_p q_p \qquad [11]$$

The methodology concerning encapsulation is similar to attack and parasitism rates, however, here the population of concern is now the parasite. With this in mind the encapsulation rate for the colony is:

$$p_e = \frac{a_3}{a_2+a_3} \qquad [12]$$

Further, using a slightly different FPC a variance estimate for p_e is:

$$\mathrm{var}(p_e) = \left(\frac{p_a\bar{y}-a_2}{p_a\bar{y}}\right)\left(\frac{(p_a\bar{y})p_e q_e}{a_2+a_3}\right) \qquad [13]$$

The value of $p_a\bar{y}$ estimates the parasite population on a per colony basis and a_2 representing the sample size analagous to n_1 in equation 11.

This concludes the derivation of colony level parasitism parameters and with the inclusion FPC's applies well to samples taken in the tent caterpillar-webworm system because of their colonial nature. In cases where the sample frequency is, or can be assumed to be, less than 5% the FPC can be dropped from variance estimates. In this example all variance calculations include FPC's. This is due to the fact that early in the host generation correction factors may only reduce negligible amounts of variance (i.e., with a sample frequence of < 5%). However, as the generation progresses the FPC becomes more significant and is retained throughout calculations for continuity and generality.

MULTISTAGE PARASITISM ESTIMATES

Methods derived at the colony level can further be applied to subplot, plot, and regional levels of the study area. This type of sampling program is termed a multistage or nested design. Calculation of mean values for each level is straightforward in that for any level, estimates are derived as a mean from the next lower level. For example, a subplot parasitism mean ($\bar{p}_p$) is the summation of the colony estimates divided by the number of colonies sampled (n_c) or:

$$\bar{p}_p = \frac{1}{n_c} \sum_{i=1}^{n_c} p_p \qquad [14]$$

Calculation of variance terms at any level is equally straightforward as mean estimates. Each level contains components of variance from lower levels. In order to clarify this relationship further an analysis of variance table is presented (Table E.1). The reader should notice that variance components are additive. Subplot parasitism variances are the sum of colony and subplot variance such that:

$$\mathrm{var}(\bar{p}_p) = \left(\frac{n_c - n_c}{N_c}\right)\left(\frac{S_{p_a}^{\ 2}}{N_c}\right) + \left(\frac{\bar{y}(\bar{y}-n_i)}{n-1}\right) p_p q_p \qquad [15]$$

Equation 15 then includes the between colony variance (subplot) with an FPC to take into account the proportion of the colonies sampled in that subplot. The FPC in this case is $N_c - n_c / N_c$ where N_c is the total number of colonies in the subplot and n_c, the number sampled. The within colony variance (Eq. 11) is added directly to determine the subplot variance estimate. These methods can extend to the plot level where needed, with an additional variance component included as defined in Table E.1.

Table E.1. ANOVA table for components of variation in parasitism rates.

Source of Variation	df	Components of Variance
Total	$N_s n_c n_1 - 1$	
Plots	$n_s - 1$	$s_c^{\ 2} + n\ s_s^{\ 2} + n_c n_1 s_p^{\ 2}$
Subplots	$n_s(n_1 - 1)$	$s_c^{\ 2} + n_1 s_s^{\ 2}$
Colonies	$n_s n_c (n_1 - 1)$	$s_c^{\ 2}$

APPENDIX F

SPECIES CONCEPTS IN THE FALL WEBWORM

SPECIES CONCEPTS IN THE FALL WEBWORM

Since Lyman's (1902) original treatment of the genus *Hyphantria* there has been continual reference made as to taxonomic status of black and red headed "races" (BH and RH). In fact, in Lyman's work 2 distinct species were recognized *H. cunea* Drury (BH) and *H. textor* Harris (RH). Since that time the dichotomization of *Hyphantria* has been retained by the recognition of species, subspecies, or races. Morris (1963) comments; "The taxonomic status of the webworm with light-headed larvae is not yet clear. In population studies, at least, it should be treated as a separate species." He states further, "This webworm (RH) and *cunea* (BH) may prove to be sibling species, occurring sympatrically from New Brunswick to Georgia." These ideas are given additional substance when other characters such as feeding rhythms, methods of web construction, diapause inducing photoperiods, lengths of larval development, and range of host plants are considered (Oliver 1963, Ito and Warren 1973). On the other hand, each of these studies has, by design or by convenience, utilized populations which occur toward the extremes in the range of the *webworm*. Thus, populations from New Brunswick and Nova Scotia are compared with those from Georgia and Arkansas. This, in effect, produces some rather striking differences in those characteristics mentioned even though BH and RH individuals, when mates, produce viable *intermediate* offspring (Morris 1963, Ito and Warren 1973). Because of these rather obvious differences questions arise as to the taxonomic placement and more importantly, treatment in population studies. The approach taken here will synthesize the available information with reference to possible changes in population make-up in response to gross climatic differences for different parts of North America. The objective of this discussion is not to solve the problem but to view the webworm in light of basic postulates concerning the species and its variability. Also, it allows us to place the Michigan population in relation to others in North America.

As mentioned above, the view taken to date has been one of discretizing the BH and RH components of the FWW. This is quite understandable if we compare entities from the extremes in its range. However, taking the data supplied by Warren and Tadic (1970), Ito and Warren (1973), Hattori and Ito (1973), and Morris (1963) provides quite a different picture. Figure F.1 presents 2 types of information. First the bar graphs located in Nova Scotia, Michigan, and Georgia picture the continuous nature of head color. The x-axis of each is a color continuum ranging from black to red and y the frequency of phenotype. It is clear from the Nova Scotia and Georgia plots (Morris 1963) that populations tend toward the BH penotype in the north while RH is favored in the south. Michigan apparently represents an intermediate with a distribution not significantly different from normal ($\chi^2 = .1838$, 3 df) (data from this study). Looking at Morris' temperature treatments it is intuitive that this might occur. A colony from the Nova Scotia population was reared under different temperature regimes in the laboratory and resulted in significant phenotypic shifts (Table F.1). This indicates a classic example of melanistic variation which occurs in many other insects in response to changes in latitude and/or altitude, hence temperature (Merritt 1970, Zuska and Berg 1974). This trend continues throughout Canada and the United States when looking at data supplied in Warren and Tadic (1970). The ratios (BH:RH) in Figure F.1 present these data. Data from Washington and Kansas indicate colonies which became mixed

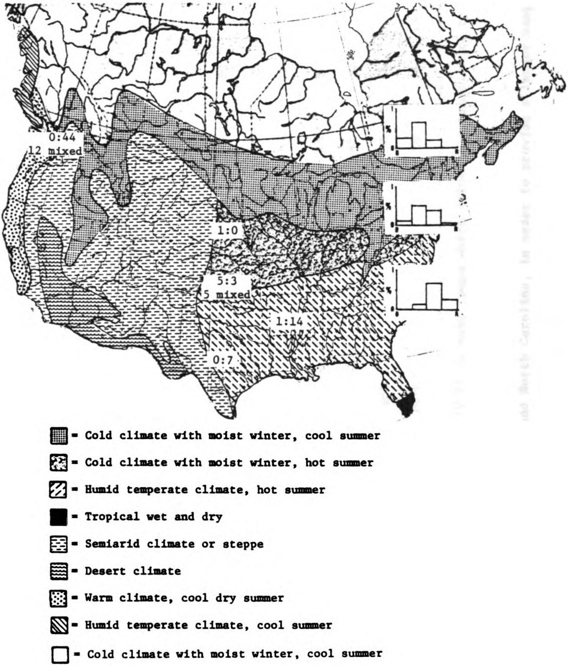


Figure F.1. Distribution of FWW head capsule color.

Table F.1. Relation of color in the fifth-instar larva of the fall webworm to temperature and collection area.

Series	Source	Treatment	Percentage of Larvae Very Light	 Light	 Medium	 Dark
a	Nova Scotia	Reared: 70-95°F[1]	0	65	35	0
b	" "	" 70-85°F[1]	0	58	42	0
c	" "	" 70°F	0	9	86	5
d	" "	" 64°F	0	0	0	100
e	" "	" 52°F	0	0	0	100[2]
f	Nova Scotia	Collected in field	0	18	62	20
g	Georgia[3]	Collected in field	25	65	10	0
h	Georgia[4]	Reared: 70°F	0	36	64	0
i	Georgia x N.S.[5]	Reared: 70°F	0	18	76	6

[1] Reared at 70 F, but exposed during instars IV-VI to heat lamps which raised air temperature to the higher value for 6 hours each day.

[2] Darker than in Series (d).

[3] Includes some larvae collected in Florida and North Carolina, in order to provide a larger sample of the southern form.

[4] Progeny of Series (2) in Table 1.

[5] Progeny of Series (4) in Table 1.

(From Morris 1963)

in transit (12 and 5, respectively). The data were derived from sample colonies taken from these various areas and classified only as to BH or RH. Even with this restricted classification the same pattern emerges with BH favored in colder climes. In addition to the frequency of BH and RH phenotypes Figure F.1 also shows a gross climatic classification of North America (Danks 1978) which supports the hypothesis of temperature induced melanization.

Until this point I have only discussed head color as an indicator of population type and this has been the approach taken by other authors. The implicit assumption has been that head color, behavioral characters, and other variables were somehow genetically associated, presumably through pleiotropism. Therefore, the BH "race" is equated with loosely formed webs, day and night feeding, a shorter developmental period, and a diapause inducing photoperiod of 10-14 hrs. While the RH group is associated with compact webs, nocturnal feeding, a longer developmental period and a critical photoperiod of 10-14 hrs. While the RH group is associated with compact webs, nocturnal feeding, a longer developmental period and a critical photoperiod of 18 hrs. These equations counter the ideas of clinal attributes in populations and numerous examples of character gradation (Dobzhansky 1970). Morris' temperature experiment demonstrates environmental intervention yet color and all other characters are considered as one. Additional studies by Morris further support the idea of clinal changes (Morris and Fulton 1970a,b, Morris 1971). Selection pressure due to temperature has been shown to truncate the distribution of adult emergence with early emerging individuals favored in cool years and late individuals in warm years (Morris and Fulton 1970a, b). This tends to explain not only the later emergence of RH individuals but also changes in melanism from one population to another. It may well be that developmental rates are also selected for by the temperature regime and hence correlated with head color.

These data suggest that the FWW represents a highly variable species showing clinal changes on climatic gradients. The fact that intermediate forms occur (behaviorally and otherwise) in Michigan, New Brunswick and Vancouver tends to invalidate the 2 "race" concept. In addition, the 2 race idea provides only a static view of a gene system which may be evolving in a number of directions. This does not negate the possibility of a pleiotropic gene but at this point there is no data to back the assumption. It is more reasonable to assume that a number of genes are operating forming the observed continuum of phenotypes and that they are highly correlated through spatial and temporal selection pressures such as temperature. This points to the need to view webworm populations, or animal and plant populations in general, as heterogeneous assemblages. Whether or not our goals are of a taxonomic nature, aimed at population processes or in a management mode we cannot consider things as only "black or red." As Wellington (1977) points out, the need is to return the insect to insect ecology: "Insect populations no longer appear to be inert masses passively responding to changing environmental pressures." The webworm problem is a classic example of the need to define the frequency distribution of phenotypes (genotypes) in natural populations. Populations exhibit a mean and variance and one without the other is meaningless.