SIMULATION OF CODLING MOTH POPULATIONS IN APPLE ORCHARDS.

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ABSTRACT

A simulation model has been developed that predicts numbers and phenology of a population of codling moth, *Cydia pomonella* (L.), in an apple orchard. The model is a general insect population model based on the iterative-cohort technique. It operates at two time scales: a fine time scale (one hour) for temperature-dependent physiological processes, and a coarse time scale (one day) for population processes. The population is divided into a specifiable number of stages, and each stage is described by four process functions, which may be of any convenient mathematical form, and may differ among stages. Each stage is divided into cohorts of individuals born or emerged on the same day, and individuals within a cohort are considered probabilistically identical. The model simulates the processes of development, transition among stages, and mortality by using probability distributions representing these processes, and incorporates the effects of pesticides on mortality of the insect. Model output was evaluated by comparison with records of pheromone trap catches of codling moths in commercial apple orchards in North Carolina. The model predicts timing of the first spring flight well, depending on the initial age distribution used. Time between peaks of numbers of adults in the model is about 15 days longer than the observed period between flight peaks in orchards. Sensitivity analysis indicates that this discrepancy may be related to differences between measured ambient temperature and tree canopy temperature. The sensitivities of numbers of insects produced by the model and timing of peaks in numbers present were determined for each of the parameters in the model. The parameters with greatest effect on the model output were those which control the locations of developmental rate functions and survival functions on the temperature scale. In the model, pesticides had a much larger effect on numbers of adults present than records of moths caught in pheromone traps indicate actually occurred, suggesting that moths caught in traps in commercial orchards where effective pesticides are applied may be largely immigrants.

INTRODUCTION

Available models of population dynamics of codling moth, *Cydia pomonella* (L.) (Lepidoptera: Olethruetidae) have been concerned either with the numbers of moths on a time scale of generations (Brown et al., 1978), or with the phenology of moths within a season (Falcon et al., 1976; Welch et al., 1978; Jorgensen et al., 1979). There are no previously published models of both numbers of moths and phenology within a season. Such a model could be of considerable use to the managers of orchards of fruit and nut trees where codling moth is a primary pest, by allowing improved evaluation of the need for pesticide application and of optimal timing of the application.

We present here a generalized model of insect population dynamics, together with details of its parameterization and its evaluation for codling moth in apple orchards. The model is based on the iterative-cohort approach (Curry et al., 1978), generalized to include an arbitrary number of stages as well as the effects of pesticides or other extrinsic mortality factors. This approach allows incorporation of detailed and realistic submodels of biological processes and their interactions with environmental conditions. The

advantages of such an approach have been discussed in more detail elsewhere (Shaffer, 1984).

The model has been evaluated by comparison with records of pheromone trap catches of codling moths in commercial apple orchards in North Carolina, and we have examined the sensitivity of the model to changes in the values of its inputs and its parameters. In particular, the effects of pesticides on codling moth phenology are examined, and implications for pest management are considered. Sensitivity analysis, together with comparison field observations, indicates which parameters are of greatest importance in prediction of numbers and phenology of codling moths, as well as the importance of microenvironmental gradients and of exogenous individuals.

THE MODEL

The model divides the insect population into stages chosen to suit both the biology and the management practicalities of the system under consideration. For codling moth, six stages were used (see Fig. 1): (1) wintering, (2) egg, (3) searching, (4) larval, (5) pupal, and (6) adult. The wintering stage includes a portion of a larval instar plus a pupal instar. The searching stage is actually a portion of the first larval instar, but is considered separately because of its susceptibility to pesticides. Wintering individuals initialize the model and produce adults; however, the model does not consider the entry of larvae into diapause, so wintering individuals are not produced by the model.

Each stage is divided into cohorts of individuals that enter the stage on a given day (Curry et al., 1978). All individuals in a cohort are considered to be probabilistically identical. At any given time t each cohort is characterized by two state variables: $a_{ij}(t)$, the physiological age or maturity of cohort j within stage i ; and $N_{ij}(t, a)$, the number in the cohort which are of age a . While this notation is redundant, since all members of a cohort are of the same age, it is retained for clarity. The desired output of the model is $N_i(t)$, the total number in stage i , which is obtained simply by summing over the cohorts.

The dynamics of cohort development are expressed in terms of the following four process functions, whose values are supplied by submodels (see section on Process Functions):

- $r_i(T)$: Rate of development within stage i as a function of temperature T (for adults, this is inverse of longevity).
- $c_i(T)$: Expected total production of stage i , as a function of temperature. For immatures this is survivorship (probability of survival) from stage i to stage $i+1$; for adults it is the number of eggs produced.
- $P_i(a)$: Cumulative fraction of production of stage i up to age a . For immatures it is the fraction which have passed to stage $i+1$; for adults it is the fraction of total egg production that has occurred.
- $F_i(a)$: Cumulative fraction of individuals lost from stage i due to death plus stage transition, up to age a .

Figure 2 shows the sequence of computations. The model operates on two time scales: a finer time scale for the temperature-dependent processes, and a coarser time scale for updating of cohorts. The increment of development (accumulation of maturity), Δa_i , is computed for each stage i for each day by summing the rate of development for each hour:

$$\Delta a_i = \sum r_i(T(t)) \cdot \Delta t,$$

where $T(t)$ is temperature at time t , and Δt is the increment of time, e.g. 1/24 day. Similarly, an average production level, $\bar{c}_i$, is computed for each day based on the production level for each hour:

$$\bar{c}_i = \sum c_i(T(t)) \cdot \Delta t.$$

Once per day, each cohort is updated based on the change in the cumulative loss function which occurred during the past day:

$$N_{ij}(t+1, a_{ij} + \Delta a_i) = N_{ij}(t, a_{ij}) \cdot S_i(t) \cdot \left[\frac{1 - F_i(a_{ij} + \Delta a_i)}{1 - F_i(a_{ij})} \right]$$

where $S_i(t)$ is the extrinsic survivorship of stage i (i.e. 1 - mortality due to factors not included in F_i on day t). If the number in a cohort drops below some small threshold value then the cohort is deleted from the population. Note that the number of cohorts may differ among stages. Number produced in the next stage, k , by cohorts in stage i is the product of total expected production averaged over the day and fraction of total production which occurred during the day, summed over all cohorts j in stage i :

$$N_{k,new}(t+1, 0) = \bar{c}_i \sum N_{ij}(t, a_{ij}) \cdot \left[\frac{P_i(a_{ij} + \Delta a_i) - P_i(a_{ij})}{1 - F_i(a_{ij})} \right]$$

where $k = 6$ for $i = 1$, $k = i+1$ for $i = 2$ to 5, and $k = 2$ for $i = 6$. A new cohort is created in each stage if any individuals have been produced in that stage during the day.

The model does not include diapause induction, photoperiodic effects on diapause termination, interaction with pheromone traps, or wintering mortality. Density-dependent factors, which were central to the model of Brown et al. (1978), are not considered, as this model is intended to be relevant to commercial orchards, where codling moth densities must be kept sufficiently low that such factors are negligible. Immigration and emigration are also not included in the model.

THE PROGRAM

The algorithm has been implemented in Pascal, and has been run on both a micro-computer and on an IBM 3081 computer. The source code is given in Appendix C.

All insect specific features are contained in the four process functions having as arguments stage number and either temperature or maturity, which can be separately compiled and linked with the main program, as shown in Fig. 2. The number of stages in the model, and the pattern of stage succession are read in as data. Initial conditions consist of

an arbitrary number of cohorts, with the stage, number of individuals, and maturity for each initial cohort read as data. Two data files are read for each day of the simulation: the first contains hourly temperatures, and the second contains the survivorship for each stage resulting from extrinsic factors such as pesticides.

The simulation was always run from January 1 to December 31 of each year. Total number of larvae generated during the year was determined by summing the number in the new larval cohort for each day over the entire simulation. The location of each peak of larval and adult numbers was determined as a measure of population phenology.

THE PROCESS FUNCTIONS

The form of each of the functions $r_i(T)$, $c_i(T)$, $P_i(a)$, and $F_i(a)$ may differ among stages. However, a basic assumption is that, for each stage, the shapes of the production and loss distributions, as functions of maturity, do not depend upon the temperature regime or other external variables. This "same-shape" property has been shown to be valid for other insect species (Sharpe et al., 1977).

The choice of functional forms was made through examination of all available data relevant to the biological factors being represented. When data pertaining to codling moth were very scarce, data from other species of insects were examined. In most cases the same form was used for all immature stages. The actual parameters were then estimated from the most reliable data by linear regression, by nonlinear regression using Marquardt's algorithm (SAS Institute Inc., 1979), or fitting by eye when this was all the data justified. General forms of the functions are discussed below, while data sources and parameter values used for each function are given in Appendix A.

Developmental rate, r_i

Four functional forms were considered for developmental rate: the logistic equation reflected about $T_{\max}$, the temperature of maximum developmental rate (Stinner et al., 1974a), the two-phase equation of Logan et al. (1976), the enzyme kinetic equation of Sharpe and DeMichele (1977), and the Gaussian equation (Taylor, 1981). The reflected logistic equation and the Gaussian equation are symmetrical about $T_{\max}$, while the other equations are asymmetrical. While the asymmetrical equations are more realistic, the difficulty of obtaining experimental data at temperatures above $T_{\max}$ and the relative infrequency of occurrence of temperatures in this range in the field make this distinction less important than it might appear. For the immature stages of codling moth, data above $T_{\max}$ were very limited, and the Gaussian function fit the data well with fewer parameters than any of the other functions, and so was used.

For searching larvae, developmental period is the time from egg hatch to apple penetration. The time it takes a larva to find an apple is a function of distance travelled to the apple and rate of movement, which depends on temperature. Rate of larval movement was modeled using a quadratic function.

Developmental rate of adults was considered to be the inverse of longevity. This was fitted by a modified logistic equation.

Total production, c_i

The production function represents total expected number of individuals of the following stage produced per individual of the current stage. For immatures, this is survival between stages, and has a value between 0 and 1. Data on survival of immature stages of codling moth as a function of temperature are scarce, with Hagley (1972) giving data on eggs, Pristavko and Degtyarev (1972) and Rock and Shaffer (1983) giving data for larval and pupal stages together, and Proverbs and Newton (1962) giving data on pupae. As none of these data sets are complete in the sense of having a wide enough range of temperatures to indicate both lower and upper thermal limits of survival, and to indicate the appropriate shape of the function near these limits, data from several other insect species were examined (Howe, 1956; Ntifo and Nowosielski-Slepowron, 1973; McDonald et al., 1980). These data indicated that the function was generally symmetrical and dropped off sharply to zero near the lower and upper limits, and thus could be adequately represented by a quadratic function. All survival rates are in the absence of pesticides; the effects of pesticides are considered separately.

For adult codling moths, the production function represents oviposition rather than survival, and thus may have values greater than one. Sexes are not represented explicitly in the model, so each individual is considered to lay one-half of the number of eggs which a female would lay, given a female/male ratio of 1. A quadratic function was also used for the oviposition versus temperature function.

Cumulative production, P_i

Transition of immatures from one stage to the next or oviposition by adults is distributed over age of members of any cohort. This distribution of production over age is described in the model by the cumulative production function which increases from a value of 0 at age 0 to a value of 1 as age becomes large. Physiological age is not directly observable in insects but is scaled according to some individual or population event. In the model, the age of immatures was defined to be 1 at the time when 50% of individuals transformed to the next stage (i.e. the median developmental period). Thus the cumulative production function is fixed at 0.5 at age 1 for the immature stages. For adults, age was defined to be 1 at the time when 50% of individuals had died (median longevity), thus the age at which the cumulative production (i.e. oviposition) function equals 0.5 is not fixed for this stage.

The distribution of developmental times has been represented by a normal distribution (Stinner et al., 1974b) and the distribution of developmental rates has been represented by a quadratic or normal function (Sharpe et al., 1977), but integration of one of these functions to form a cumulative distribution of development times would be computationally expensive. Cumulative development times were modeled using a modification of Dobie's (1978) formula

$$y = \exp[c - \exp(a - bt)],$$

where y is the cumulative emergence, t is time, and a , b , and c are constants. This was used in preference to a suggestion by Stinner et al. (1975) as it has fewer parameters and describes the data very well. In our model cumulative development is a fraction between 0 and 1, so the parameter c reduces to zero. This function was used for immature and adult stages.

Cumulative loss, F_i

No data were available for distribution of mortality over age of immature codling moths, so the assumption was made in the model that all mortality occurs at the time of transition to the next stage. Since loss from an immature stage is the sum of mortality and transition to the next stage, the cumulative loss function is identical to the cumulative production function for immatures. It would probably be more realistic if more mortality occurred at an early age in each stage, but this assumption should not affect net survivorship or production in the model; only number present in each of the immature stages would be altered if a more realistic cumulative loss function were used.

For adults, loss occurs by mortality only. The limited data on mortality distribution in adult codling moths (Howell, 1981) together with cumulative mortality distributions for other insects (Reisen et al., 1979; Butler and Watson, 1980; Moscardi et al., 1981) suggest that a logistic function reasonably approximates the cumulative loss function for a number of species. The location of this function is fixed by the definition of age as 1 at the time when 50% of adults are alive in a cohort.

PESTICIDE EFFECTS

A major goal of this work is to estimate the effects that applications of pesticides might have on the numbers and phenology of a population of codling moths in an apple orchard. The model of effects of a pesticide on a population was divided into three parts: relationship between application rate ($\text{kg}\cdot\text{ha}^{-1}$) and resulting residue on plant surfaces ($\mu\text{g}\cdot\text{cm}^{-2}$); degradation of the pesticide over time; and the pesticide residue-mortality response function.

A linear relationship should exist between application rate of any material and the resulting concentration on plant surface, given that the same volume of water is used as a carrier, that surface tension of the spray is constant, that the same sprayer is used, and the same trees are used. These and other factors can introduce a tremendous amount of variability into the relationship between rate and residue (Hall et al., 1981); but as their effects are not generally known, they were ignored and a simple linear relationship with a zero intercept was assumed. See Appendix B for data sources and slope estimate.

The degradation of pesticides has been modeled as a simple exponential decay with time (Bruhn and Fry, 1982), as a first order function of weather factors (Nigg et al., 1977; Nigg et al. 1978), and as a log-log relationship with time (Stamper et al., 1979). A model of pesticide degradation which requires inputs of weather factors beyond temperature

would not have been useful, because such data were not generally available for the sites where model evaluation was to be done. A practical problem with fitting the model of Stamper et al. (1979) is that all measurement times are scaled by the interval from application until the first measurement was taken; this time is often expressed as "immediately after the deposit had dried" (Gratwick et al., 1965), which is not usable in fitting the log-log model. For these reasons the simple first-order, exponential decay model was used; this model does explain most of the variation in deposit over time (Stamper et al., 1979). Data sources and decay rate estimates for pesticides applied in the orchards used for model evaluation are given in Appendix B.

The relationship between pesticide residue and resultant mortality has been modeled in some detail by Casagrande and Haynes (1976) and by Jones et al. (1977); both models consider a dose of pesticide to be absorbed by an insect at a rate proportional to concentration to which the insect is exposed (i.e. residue for a surface-dwelling insect). Data necessary to fit one of these models are not generally available, however, so the widely-used model of a linear relationship between probit of mortality and log of residue (Gratwick et al., 1965) was adopted. Data sources and parameter estimates for this model are given in Appendix B. Most experimental studies of pesticide effects on codling moth have dealt with first-instar larvae (Barnes, 1958; Hameed and Allen, 1976; Fisher and Menzies, 1979). While there is evidence that pesticides can cause mortality of larvae for a few days after they enter apples (Hough, 1962; Gratwick and Tew, 1966), the larva in the apple is considered to be relatively protected from pesticide mortality (Rock, 1976). There are few data on toxicity of pesticides to egg, pupa, or adult stages (some exceptions are Hamilton et al., 1954; Brunson and Dean, 1963; Gratwick and Tew, 1966; Hagley, 1975; Pree and Hagley, 1977; Hoying and Riedl, 1980; Gaunce et al., 1980), but newly hatched larvae are generally the stage most susceptible to pesticide mortality (Brunson and Dean, 1963). Thus, only searching larvae are subject to pesticide mortality in the present model.

When more than one insecticide was applied to an orchard, the resultant survivorship was computed as the product of the survival that would have resulted from each pesticide alone, i.e. mortality from different materials was considered to be independent of the others.

Records of pesticide applications in commercial apple orchards in Henderson Co., N.C. (Sutton et al., 1983) were used to estimate the residue level of each pesticide used on each day of the year. When a spray was applied, the previous residue was added to the residue resulting from the spray. The survival resultant from each pesticide present was computed using the probit-log residue model, and the net survival was computed as the product of these values. These values were then stored as a file to be applied as extrinsic mortality in the population simulation.

MODEL EVALUATION

Typical behavior of all stages in the model in the absence of pesticides is shown in Fig. 3. The output is reasonable in that there are three peaks of adults (Rock and

Yeargan, 1974), and the numbers of individuals does not increase excessively between generations. Number of individuals in each stage changes relatively smoothly, except for the searching stage. This stage lasts a short period (mean 0.107 days at 27.4°C), so the number present in the stage is strongly dependent on short-term temperatures.

The model was evaluated by comparison of simulated number of adults with records of pheromone trap catches of male codling moths from commercial apple orchards in Henderson County, N.C. (Shaffer and Rock, 1983). No data on abundance of other stages were available. The model was run using hourly temperature records from these same orchards (Saucier and Bragg, 1983). For simulation runs in which pesticide effects were included, mortalities were computed (see Appendix B) from pesticide records from these same orchards (Sutton et al., 1983). The simulation was started on January 1 with 100 wintering individuals in five cohorts with the following age distribution: 10 of age 0.3, 20 of age 0.4, 40 of age 0.5, 20 of age 0.6, and 10 of age 0.7. This distribution was picked arbitrarily, as we had no knowledge of actual distribution of maturity of wintering individuals; sensitivity to initial age distribution is discussed in the next section.

The number of male codling moths caught in traps in the commercial orchards was generally low, with averages over orchards of total number of moths caught per trap during the entire year ranging from 17.2 to 33.8, depending on the year. The number of traps per orchard varied from 1 to 6, depending on size of the orchard (generally 1 trap per 1.2-1.6 ha), and infestation level varied among orchards and years. Because number of individuals trapped varied erratically for most traps from week to week, identification of timing of flight peaks is more reliable with a larger sample size, i.e. larger number of moths trapped. To facilitate comparison of trap records with model output, only orchard-year records with approximately 100 or more moths trapped were selected for use. Evaluation of model output in terms of number of individuals present was not attempted because the number of individuals in the model depends on the number of wintering individuals used to initialize the model. Further, there are numerous problems involved in interpreting numbers of moths captured by a pheromone trap (Howell, 1974; Riedl, 1980; McNally and Barnes, 1981).

To make the location of peaks in the pheromone trap records more distinct, the sequences were smoothed using repeated medians of 3 and "hanning" (weighted running means of 3) (Tukey, 1977). For each orchard, the dates of the two or three peaks in the smoothed records were determined, and these were compared with the dates of peaks in adult numbers in the simulation run with temperatures from that orchard, but with no pesticide mortality applied (Table 1). An example of the smoothed catch records, together with the output of the simulation model, is shown in Fig. 4. The mean deviation (simulated date minus actual date) for the first peak was -2.75 days, and the largest deviation was -14 days; for the second peak, the mean deviation was 12.0 days, and the maximum deviation was 64 days; for the third peak, the mean deviation was 28.6 days, and the maximum deviation was 42 days. The simulated date of each peak became later with respect to the actual date as the season progressed. While the mean deviation was low for the first peak, and within the range of uncertainty of the actual date of the peak, the mean deviation was larger for the second peak, and quite large for the third peak. The

interpeak interval was greater in the model than in reality, by about 15 to 16 days.

For each of the orchard-year combinations in Table 1, the simulation was also run with the mortality effects of pesticides included. The effects of pesticides on numbers and timing in the simulation output varied from slight, with numbers reduced somewhat and phenology essentially unchanged (Fig. 5), to severe, with almost no individuals present after the initial adult flight period (Fig. 6). For cases in which pesticides eliminated later peaks in the simulation output, the pesticides do not appear to have had correspondingly strong effects on the actual flight records. In the seven cases for which a second peak in adult numbers remained, the second peak was shifted 3 to 22 days later by pesticide application. In four cases, the absolute error of date of the second peak increased, and in three cases it decreased. Thus application of pesticides tended to delay simulated timing of peaks of numbers, when peaks remained visible.

SENSITIVITY ANALYSIS

For all of the sensitivity studies described below, a typical set of field temperature data was used for all simulation runs. Three measures of model performance (outputs) were used to evaluate sensitivity: total number of larvae produced during the simulation, date of the first peak of larvae, and date of the second peak of adults (first peak of adults was not used as those adults are produced directly from the wintering stage). Change in number of larvae was evaluated on a relative basis, as percent change from number in the standard run. Changes in dates of the peaks were evaluated in absolute terms, i.e., number of days changed from the standard run.

Sensitivity of the model output to initial conditions was examined by running the simulation with various initial age distributions of the wintering stage. Model output using the same initial age distribution as used for model evaluation, with 5 cohorts of ages from 0.3 to 0.7 centered at age 0.5, was compared with output using a single cohort of age 0.5; there were no differences in location of any of the larval or adult peaks or in the total number of larvae produced by the model. Additional runs were made with a single initial cohort with age ranging from 0.0 to 0.8; as age of the initial cohort increased, the first adult peak came earlier and the total number of larvae decreased. For an increase of age of the initial cohort by 0.1 (with initial age in the area of 0.5), date of the first adult peak decreased by about 11 days and total numbers decreased by about 21%. Total numbers were lowered apparently because stages following the wintering stage suffered increased mortality due to low temperatures early in the year.

Sensitivity of the model output to changes in values of its parameters was determined by running the model with each parameter individually increased and then decreased by 10% from its standard run value. For each output of the model and each parameter the average effect of a 10% change in parameter value and an index of non-linearity were computed as:

$$e = \frac{1}{2}[F(1.1p_0) - F(0.9p_0)]$$

and

$$n = \frac{1}{2}[F(1.1p_0) + F(0.9p_0)] - F(p_0),$$

where $F(p)$ is the model output with the parameter at value p , and p_0 is the standard run value of the parameter. The average effect is proportional to a numerical approximation to the partial first derivative of the output with respect to the parameter, and the nonlinearity is proportional to an approximation to the partial second derivative. In the discussion, we will make use of the fact that for a parameter which varies, the nonlinearity index is a measure of the difference between the average output and the output evaluated at the average value of the parameter. For a linear function, this difference is zero.

These values are presented in Table 2. For the total production functions and the rate function for searching larvae, the quadratic function was described by $T_{\max}$, the temperature of the maximum of the function, T_{σ} , the change in temperature from $T_{\max}$ to produce a value of the function of zero, and $R_{\max}$, the value of the function at $T_{\max}$. These parameters are analogous to those for the Gaussian functions for developmental rate, and changes are easier to visualize than changes in the standard parameters.

For most parameters and outputs, the nonlinearity was smaller than the average effect, indicating a largely linear relationship between the parameter and the output. The exceptions to this were the effects of $T_{\max}$ and T_{σ} parameters of the wintering stage on total number of larvae. A shift in $T_{\max}$ for any of the rate or total production functions means that the entire function was shifted on the temperature axis. While shifting $T_{\max}$ of the wintering stage to a lower temperature results in a longer period for population growth by the other stages, it also results in adults emerging at temperatures in which oviposition is reduced and mortality of eggs and larvae is high, thus reducing the net number produced. Increasing T_{σ} of the wintering stage has a similar effect, by increasing the development rate at low temperatures. The moderately high nonlinearities of number of larvae with $T_{\max}$ of developmental rate of eggs, larvae, and pupae may result from similar effects of increasing mortality early in the year. Effects of parameter changes on dates of occurrence of peaks were generally small; the largest effects were by the $T_{\max}$ parameters of wintering, egg, larval, and pupal stages, and the T_{σ} parameter of the wintering stage. These all had strong effects by affecting the rate of development of the immature stages in the temperature ranges experienced by the stages. Parameters of development rate of the searching stage had essentially no effect on any output measure, because developmental period remained much less than a day regardless of parameter changes. Uniform positive effects on total number of larvae of $R_{\max}$ and T_{σ} parameters of the total production functions were expected, as increases in these parameters result in higher overall survivorship, and in higher survivorship over a wider range of temperatures, respectively. Parameters of all functions except developmental rate had very small effects on dates of peaks; however, large temporal changes in survivorship caused by pesticides can have large effects on phenology, as seen above.

Model sensitivity to parameter changes was also determined under an actual regime of pesticide applications, considered to be typical. In this regime, 10 sprays were applied between day 114 and day 227, at intervals of 3 to 16 days. The first application was prolate (50 WP, 1.68 kg·ha⁻¹), the fourth application was azinphosmethyl (50 WP, 0.84 kg·ha⁻¹), and the remaining applications were parathion (15 WP, 2.69 or 3.36 kg·ha⁻¹).

Expected mortality of the searching stage from these applications was computed, and is shown with the simulation results using these survival values in Fig. 7. Total number of larvae produced was reduced by 95.5% from the standard run without pesticides. Time of the first larval peak was delayed by 1 day, and the second adult peak was delayed by 10 days, compared with the standard run without pesticides. For most parameters and outputs, the sensitivities were similar to those without pesticides. The largest differences were in the sensitivity of total number of larvae produced to T_{σ} and $T_{\max}$ of development rate of the wintering stage; average change of total number was 94% for a 10% change in $T_{\max}$, and -45% for a 10% change in T_{σ} . An increase in $T_{\max}$ or a decrease in T_{σ} would slow development, and thus delay peaks; since pesticide applications ended on day 227, delaying population growth allows the later generation to avoid pesticides, and thus have higher survival. The effects of four other parameters on number of larvae also changed signs: slope of the cumulative production function to -8%, $T_{\max}$ of the development rate of the egg stage to 8%, location of adult development rate to 8%, and slope of adult development rate to -7%. All of these changes apparently result from alteration of the overlap of periods of high pesticide mortality with times of peak numbers of the searching stage, and thus are probably very dependent upon the precise pesticide schedule used. Thus the optimal timing of pesticide applications to maximize mortality would be very sensitive to actual timing of temporal patterns of abundance of susceptible stages.

None of the average effects on timing of larval or adult peaks change signs with pesticide application, but it was observed above that pesticide applications tended to delay timing of peaks. To further explore the relationship between reduction in numbers of larvae produced and delay in date of the second larval peak caused by pesticide application, these values were determined for pairs of simulations run with and without pesticide applications. $\log_{10}$ reduction of total larval numbers ranged from 0.17 to 4.9, and delay of the second larval peak ranged from 1 to 47 days. The two measures were positively correlated ($r = 0.51$, $P < 0.05$), but there was considerable scatter in the relationship. The delays probably occurred because the sprays generally ended early enough that considerable population growth could occur after pesticide application ended, while variability in the delays occurred because of large variations in number and timing of applications among orchards and years.

DISCUSSION

In order for a model of insect pest population dynamics to be directly useful as a management tool, it must be driven by observations which are reasonably accessible, and must predict number of individuals versus time with sufficient accuracy to permit decisions to be made as to the need for and the timing of control procedures. Previously published models of codling moth evaluated for North Carolina have been quantitatively unsatisfactory and, in some cases, even qualitatively inaccurate (Shaffer and Rock, 1983).

The present model has been evaluated using observed environmental and control inputs, but without input of observations on the insect population. Parameters have been taken from laboratory data, as described in the Appendices. These *ab initio* calculations

are in qualitative agreement with observations, but do not have sufficient predictive accuracy to serve as a guide for timing of chemical treatment. However, because of the degree to which biological detail is incorporated into the model, the disagreement allows us further understanding of the system dynamics and suggests useful directions for improvement.

There are two main points of disagreement between simulation results and observation: simulated times between peaks of the adult population are an average of 15 days longer than observed, and for many pesticide application regimes, the simulated results fail to show the observed second generation.

Examination of the sensitivities reported in Table 2 shows that the most likely source of the timing discrepancy concerns the parameter $T_{\max}$ for larval and pupal development. Note that while $R_{\max}$, the height of the development vs. temperature curve, and T_0 , which affects its steepness, affect total numbers of larvae produced, they have very small (and linear) effects on adult peak timing.

Developmental rate parameters for larvae and pupae were based on four sets of data from sites spread around the world. The developmental rate of larvae from North Carolina at 16°C was 89% higher than from U.S.S.R. (Pristavko and Degtyarev, 1972) and 58% higher than from Canada (E.A.C. Hagley, personal communication, 1982); the developmental rate at 32°C was higher in North Carolina than has been reported from other areas for temperatures above 29°C. Such comparisons raise the possibility of genotypic variability in the relationship of developmental rate and temperature. Moreover, for each of these studies, data points were sparse at the higher temperatures, so that accuracy of determination of $T_{\max}$ may be poor. The sensitivities reported in Table 2 are based on a $\pm 10\%$ variation, which in the case of $T_{\max}$ for developmental rate of larvae and pupae is about 5°C. Evidently, an error of -2.5°C in the two $T_{\max}$ values would account for the discrepancy. Such an error is certainly within the accuracy of the data.

A second likely source of error related to $T_{\max}$ is the difference between ambient weather station temperatures, used to drive the model, and the internal fruit and cocoon temperatures experienced by developing larvae and pupae. From the description of the functional forms in the Process Function section, it is evident that an error in estimating local temperature is equivalent to an error in $T_{\max}$ of the same magnitude, but of opposite sign. The studies of Anderson (1967), Landsberg et al. (1973), and Thorpe (1974) have shown that leaf and fruit temperatures may differ by as much as 13-14°C from ambient air temperature. If we were to assume that the mean daily internal fruit and cocoon temperatures are the same as at the weather station, but that equal amounts of time are spent at 5°C higher and 5°C lower than ambient, the nonlinearities of larval and pupal developmental rates would be sufficient to account for the discrepancy. The importance of the nonlinearity effect makes it unlikely that a linear degree-day model would be useful, and may be related to the proportion of time near the extremes of the rate versus temperature curve.

To summarize, the average difference between simulated and observed interpeak interval is most likely attributable to a combination of error in the determination of $T_{\max}$ and differences between local and measured temperature. More detailed temperature

sensitivity studies are currently being conducted, and will be reported separately. An additional effect, which has not been dealt with in this model, is the possible effect of photoperiod on developmental rate (Rock and Shaffer, 1982).

The other major point of disagreement between simulations and observations concerns persistence of later generations in the face of pesticide usage. The model indicates that large changes in mortality due to pesticides may eliminate later generations, or shift their timing if they are not eliminated. There is, however, no evidence from records of pheromone trap catches in commercial orchards that pesticide applications actually have such effects. The implication is that pheromone trap catches consist largely of immigrant moths from populations outside the orchards. Immigration of codling moths is difficult to quantify (Suski et al., 1981), and may be impossible to control. Further, if the source population is outside of the orchard, then the size of the population will vary due to fluctuating natural mortality sources (Ferro et al., 1975).

Another point which requires discussion is the initial physiological age distribution assumed for wintering individuals. We note that diapaused larvae do not completely cease biological activity. Given the laboratory data available for developmental rates and the relative mildness of North Carolina winters (compared to other apple growing areas), it is reasonable to expect a certain amount of development to have taken place before January 1, the date at which simulations were begun. As pointed out in the Sensitivity Analysis section, the distribution used is equivalent (with respect to model output) to starting with a single cohort of age 0.5, and results in good accuracy of timing of the first adult peak. Varying the age of this initial cohort varies the timing of the first peak but leaves the remaining dynamics unaffected.

CONCLUSIONS

It seems unlikely that a population dynamic model, at least for codling moth, will be of value as a management tool if the model does not take account of microenvironment and of immigration. We can suggest at least three ways in which microenvironment may be accounted for:

- Direct measurement. At one time it would have been preposterous to suggest that a farmer go to the expense of temperature probes to measure tree canopy temperatures. Increased availability of the sensing and data processing equipment, however, makes it reasonable to begin examining the benefit/cost ratio for such direct methods.
- Mathematical models. It may be possible to develop an index which would relate canopy environment to weather station temperatures. Such an index would have to take account of wind, humidity, cloudiness and canopy density.
- Measurement on "surrogate" variables, such as fruit development or development of other insects. Such measurements would be used in conjunction with a model of the system dynamics to calibrate the orchard against weather station temperatures. An appropriate formalism for combining information from models of system dynamics with information from measurements is that of the Kalman

filter algorithm (see, for example, Zaveleta and Dixon, 1982).

A possible approach to handling the immigration problem is to simulate the insect dynamics with the history of pesticide applications to represent the indigenous population, and again without pesticide to represent the timing of the exogenous population. Pheromone trap measurements might then be used to estimate the relative weighting to be placed on each. The Kalman filtering concept might be of value here in combining system models with the history of observations, so as to estimate the number of immigrants being provided by the exogenous population.

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REFERENCES

- Anderson, R.W., 1967. Air temperatures in an apple tree. M.S. Thesis, Department of Meteorology, Penn. State Univ.
- Barnes, M.M., 1958. Technique for testing insecticide deposits with newly hatched codling moth. *J. Econ. Entomol.*, 51: 547-549.
- Brown, G.C., Berryman, A.A. and Bogyo, T.P., 1978. Simulating codling moth population development, validation, and sensitivity. *Environ. Entomol.* 7:219-227.
- Brown, M.R. and Brown, J.J., 1982. Effect of methoprene on the fecundity and fertility of the codling moth. *Ann. Entomol. Soc. Am.*, 75: 257-260.
- Bruhn, J.A. and Fry, W.E., 1982. A mathematical model of the spatial and temporal dynamics of chlorothalonil residues on potato foliage. *Phytopathology* 72: 1306-1312.
- Brunson, M.H. and Dean, F.P., 1963. Bioassay of the toxicity of insecticide residues to the codling moth in apple orchards. U.S. Dept. Agric. ARS-33-90. 10 pp.
- Butler, G.D., Jr. and Watson, F.L., 1980. Simulating the longevity of adult pink bollworms. *Ann. Entomol. Soc. Am.* 73: 158-159.
- Casagrande, R.A. and Haynes, D.L., 1976. An analysis of strip spraying for the cereal leaf beetle. *Environ. Entomol.* 5: 612-620.
- Chiba, M., Phillips, J.H.H. and Roberts, M.D., 1978. Lethal residues of seven insecticides for control of tarnished plant bug determined by four methods. *J. Econ. Entomol.* 71: 369-372.
- Curry, G.L., Feldman, R.M. and Smith, K.C., 1978. A stochastic model of a temperature-dependent population. *Theor. Pop. Biol.* 13: 197-213.
- Deseo, K.V., 1971. Study of factors influencing the fecundity and fertility of codling moth (*Laspeyresia pomonella* L., Lepid., Tortr.). *Acta Phytopath. Acad. Scient. Hung.* 6: 243-252.
- Deseo, K.V., 1973. Side-effect of diapause inducing factors on the reproductive activity of some lepidopterous species. *Nature New Biol.* 242: 126-127.

- Dobie, P., 1978. A simple curve describing the development pattern of some beetles breeding on stored products. *J. Stored Products Res.* 14: 41-44.
- Falcon, L.A., Pickel, C. and White, J., 1976. Computerizing codling moth. *Western Fruit Grower* 96: 8-14.
- Ferro, D.N., Sluss, R.R. and Bogyo, T.P., 1975. Factors contributing to the biotic potential of the codling moth, *Laspeyresia pomonella* (L.) in Washington. *Environ. Entomol.* 4: 385-391.
- Fisher, R.W. and Menzies, D.R., 1979. Pickup of phosmet wettable powder by codling moth larvae (*Laspeyresia pomonella* (Lepidoptera: Olethreutidae)) and toxicity responses of larvae to spray deposits. *Can. Entomol.* 111: 219-223.
- Garlick, W.G., 1948. A five-year field study of codling moth larval habits and adult emergence. *Sci. Agric.* 28: 273-292.
- Gaunce, A.P., Madsen, H.F., McMullen, R.D. and Hall, J.W., 1980. Dosage response of the stages of codling moth, *Laspeyresia pomonella* (Lepidoptera: Olethreutidae), to fumigation with methyl bromide. *Can. Entomol.* 112: 1033-1038.
- Gehring, R.D. and Madsen, H.F., 1963. Some aspects of the mating and oviposition behavior of the codling moth, *Carpocapsa pomonella*. *J. Econ. Entomol.* 56: 140-143.
- Geier, P.W., 1963. The life history of codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), in the Australian Capital Territory. *Austr. J. Zool.* 11: 323-367.
- Geier, P.W. and Briese, D.T., 1978. The demographic performance of a laboratory strain of codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae). *J. Appl. Ecol.* 15: 679-696.
- Glen, D.M., Milsom, N.F. and Wiltshire, C.W., 1981. The effect of predation by blue tits (*Parus caeruleus*) on the sex ratio of codling moth (*Cydia pomonella*). *J. Appl. Ecol.* 18: 133-140.
- Glenn, P.A., 1922a. Relation of temperature to development of the codling moth. *J. Econ. Entomol.* 15: 193-198.
- Glenn, P.A., 1922b. Codling-moth investigations of the state entomologist's office, 1915, 1916, and 1917. *Bull. Ill. Nat. Hist. Surv.* 14: 219-289.
- Gratwick, M., 1964. Laboratory assessments of the toxicity of field-weathered deposits of insecticides to larvae of the codling moth *Cydia pomonella* (L.). *Bull. Entomol. Res.* 55: 35-47.
- Gratwick, M. and Tew, R.P., 1966. A comparison of the toxicity of various carbamate, organophosphorus and organochlorine compounds to the codling moth. *Proc. 3rd British Insecticide and Fungicide Conference 1965, Brighton*, pp. 276-285.
- Gratwick, M., Sillibourne, J.M. and Tew, R.P., 1965. The toxicity of insecticides to larvae of the codling moth, *Cydia pomonella* (L.). *Bull. Entomol. Res.* 56: 367-388.
- Hagley, E.A.C., 1972. Observations on codling moth longevity and egg hatchability. *Environ. Entomol.* 1: 123-125.
- Hagley, E.A.C., 1973. Timing sprays for codling moth (Lepidoptera: Olethreutidae) control on apple. *Can. Entomol.* 105: 1085-1089.
- Hagley, E.A.C., 1974. Codling moth: emergence, sex ratio, and abundance. *Can.*

- Entomol. 106: 399-402.
- Hagley, E.A.C., 1975. Note on the ovicidal effect of three insecticides against the codling moth (Lepidoptera: Olethreutidae). *Proc. Entomol. Soc. Ont.* 106: 55-58.
- Hagley, E.A.C. and Chiba, M., 1980. Efficacy of phosmet and azinphosmethyl for control of major apple in Ontario. *Can. Entomol.* 112: 1075-1083.
- Hall, F.R., Reichard, D.L. and Krueger, H.R., 1981. Effects of spray volume and nozzle pressure on orchard spray deposits. *J. Econ. Entomol.* 74: 461-465.
- Hall, J.A., 1929. Six years' study of the life history and habits of the codling moth (*Carpocapsa pomonella* L.). *Ann. Rep. Entomol. Soc. Ont.* 59: 96-105.
- Hall, J.A., 1934. Observations on the behavior of newly hatched codling moth larvae. *Can. Entomol.* 66: 100-102.
- Hameed, S.F. and Allen, J.G., 1976. Toxicity and persistence of some organophosphorus insecticides and permethrin on apple fruits for the control of codling moth, *Laspeyresia pomonella* (L.). *J. Hort. Sci.* 51: 105-115.
- Hamilton, D.W., Summerland, S.A. and Fahey, J.E., 1954. Codling moth control experiments, 1950-1953. *J. Econ. Entomol.* 47: 768-775.
- Hathaway, D.O., Clift, A.E. and Butt, B.A., 1971. Development and fecundity of codling moths reared on artificial diets or immature apples. *J. Econ. Entomol.* 64: 1088-1090.
- Hathaway, D.O., Lydin, L.U., Butt, B.A. and Morton, L.J., 1973. Monitoring mass rearing of the codling moth. *J. Econ. Entomol.* 66: 390-393.
- Hough, W.S., 1943. Development and characteristics of vigorous or resistant strains of codling moth. *Tech. Bull. Va. Polytech. Inst. (Va. Agric. Exp. Stn., Blacksburg)* 91: 1-32.
- Hough, W.S., 1962. Toxicity of some insecticides to larvae of codling moth after they enter apples. *J. Econ. Entomol.* 55: 378-381.
- Hough, W.S., Stearns, L.A., Willey, C.R. and Cagle, L.R., 1926. Codling moth investigations in Virginia. *Bull. Va. Polytech. Inst. (Va. Agric. Exp. Stn., Blacksburg)* 248: 1-27.
- Howe, R.W., 1956. The effect of temperature and humidity on the rate of development and mortality of *Tribolium castaneum* (Herbst) (Coleoptera, Tenebrionidae). *Ann. Appl. Biol.* 44: 356-368.
- Howell, J.F., 1971. Problems involved in rearing the codling moth on diets in trays. *J. Econ. Entomol.* 64: 631-636.
- Howell, J.F., 1972. Rearing the codling moth on a soya, wheat germ, starch medium. *J. Econ. Entomol.* 65: 636-637.
- Howell, J.F., 1974. The competitive effect of field populations of codling moth on sex attractant trap efficiency. *Environ. Entomol.* 3: 803-807.
- Howell, J.F., 1981. Codling moth: the effect of adult diet on longevity, fecundity, fertility, and mating. *J. Econ. Entomol.* 74: 13-18.
- Hoying, S.A. and Riedl, H., 1980. Susceptibility of the codling moth to diflubenzuron. *J. Econ. Entomol.* 73: 556-560.
- Isley, D., 1938. Codling moth oviposition and temperature. *J. Econ. Entomol.* 31: 356-359.

- Jackson, D.M., 1982. Searching behaviour and survival of 1st instar codling moths. *Ann. Entomol. Soc. Am.* 75: 284-289.
- Jones, J.W., Lloyd, E.P. and Stinner, R.E., 1977. Insect population mortality: a dynamic model of insecticide effectiveness. *Environ. Entomol.* 6: 799-803.
- Jorgensen, C.D., Martinsen, M.F. and Westover, L.J., 1979. Validating Michigan State University's moth model (MOTHMDL) in an arid environment: a test in Utah. *Great Lakes Entomol.* 12: 203-212.
- Klinger, J.W., Vogel, W. and Willie, H., 1958. Der Einfluss der Temperatur auf die Eilage des Apfelwicklers. *Schweiz. Z. Obst-u. Weinbau* 67: 256-262. [Abstr. in *Rev. Appl. Entomol. A*, 49: 512, 1961.]
- Landsberg, J.J., Powell, D.B.B. and Butler, D.R., 1973. Microclimate in an apple orchard. *J. Appl. Ecol.* 10: 881-896.
- Logan, J.A., Wollkind, D.J., Hoyt, S.C. and Tanigoshi, L.K. 1976. An analytical model for description of temperature dependent rate phenomena in arthropods. *Environ. Entomol.* 5: 1133-1140.
- MacLellan, C.R., 1962. Mortality of codling moth eggs and young larvae in an integrated control orchard. *Can. Entomol.* 94: 655-666.
- MacLellan, C.R., 1963. Predator populations and predation on the codling moth in an integrated control orchard -- 1961. *Mem. Entomol. Soc. Can.* 32: 41-54.
- MacLellan, C.R., 1972. Sex ratios in three stages of field collected codling moth larvae. *Can. Entomol.* 104: 1661-1664.
- Madsen, H.F. and Williams, K., 1968. Effectiveness and persistence of low dosages of azinphosmethyl for control of the codling moth. *J. Econ. Entomol.* 61: 878-879.
- McDonald, G., McLaren, I.W., Shelden, G.P. and Smith, I.R., 1980. The effect of temperature on the population growth potential of *Culex annulirostris* Skuse (Diptera: Culicidae). *Austr. J. Ecol.* 5: 379-384.
- McEwen, F.L., Ritcey, G., Braun, H., Frank, R. and Ripley, B.D., 1980. Foliar pesticide residues in relation to worker re-entry. *Pesticide Sci.* 11: 643-650.
- McMechan, A.D., Morgan, C.V.G. and Wardle, G.A., 1972. Erosion of azinphosmethyl from apple leaves by rain and over-tree irrigation. *J. Entomol. Soc. Br. Columb.* 69: 5-8.
- McNally, P.S. and Barnes, M.M., 1981. Effects of codling moth pheromone trap placement, orientation and density on trap catches. *Environ. Entomol.* 10: 22-26.
- Menzies, D.R., Pree, D.J., Fisher, R.W. and Chisholm, D., 1979. Correlation of spray coverage ratings, and phosmet residues with mortality of Oriental fruit moth larvae. *J. Econ. Entomol.* 72: 721-727.
- Moscardi, F., Barfield, C.S. and Allen, G.E., 1981. Effects of temperature on adult velvetbean caterpillar oviposition, egg hatch, and longevity. *Ann. Entomol. Soc. Am.* 74: 167-171.
- Nigg, H.N., Allen, J.C. and Brooks, R.F., 1977. Weather and pesticide residues. *Proc. Int. Soc. Citriculture* 2: 437-441.
- Nigg, H.N., Allen, J.C., King, R.W., Thompson, N.P., Edwards, G.J. and Brooks, R.F., 1978. Dislodgeable residues of parathion and carbophenothion in Florida

- citrus: a weather model. Bull. Environ. Contam. Toxicol. 19: 578-588.
- Ntifo, S.E.A. and Nowosielski-Slepowron, B.J.A., 1973. Developmental period and mortality of *Gnathocerus maxillosus* (F.) (Coleoptera, Tenebrionidae) under various conditions of temperature and humidity. J. Stored Prod. Res. 9: 51-59.
- Pree, D.J., Butler, K.P., Kimball, E.R. and Stewart, D.K.R., 1976. Persistence of foliar residues of dimethoate and azinphosmethyl and their toxicity to the apple maggot. J. Econ. Entomol. 69: 473-478.
- Pree, D.J. and Hagley, E.A.C., 1977. Toxicity of some insecticides to eggs of the Oriental fruit moth and codling moth. Proc. Entomol. Soc. Ont. 108: 69-74.
- Pristavko, V.P. and Degtyarev, B.G., 1972. The effect of temperature on the development and reproductive abilities of codling moth *Laspeyresia pomonella* (Lepidoptera, Tortricidae). 1. Experimental data. Zool. Zh. 51: 517-523. [in Russian]
- Proverbs, M.D. and Newton, J.R., 1962. Effect of heat on the fertility of the codling moth, *Carpocapsa pomonella* (L.) (Lepidoptera: Olethreutidae). Can. Entomol. 94: 225-233.
- Putman, W.L., 1963. The codling moth, *Carpocapsa pomonella* (L.) (Lepidoptera: Tortricidae): review with special reference to Ontario. Proc. Entomol. Soc. Ont. 93: 22-60.
- Reisen, W.K., Siddiqui, T.F., Aslam, Y. and Malik, G.M., 1979. Geographic variation among the life table characteristics of *Culex tritaeniorhynchus* from Asia. Ann. Entomol. Soc. Am. 72: 700-709.
- Riedl, H., 1980. The importance of pheromone trap density and trap maintenance for the development of standardized monitoring procedures for the codling moth (Lepidoptera: Tortricidae). Can. Entomol. 112: 529-544.
- Riedl, H. and Loher, W., 1980. Circadian control of oviposition in the codling moth, *Laspeyresia pomonella*, Lepidoptera: Olethreutidae. Entomol. Exp. Appl. 27: 38-49.
- Riedl, H.W., Croft, B.A. and Howitt, A.F., 1976. Forecasting codling moth phenology based on pheromone trap catches and physiological time models. Can. Entomol. 108: 449-460.
- Rock, G.C., 1976. North Carolina apple insects and mites. N.C. Agric. Ext. Serv. Circ. 600: 1-26.
- Rock, G.C. and Shaffer, P.L., 1982. Tufted apple budmoth (Lepidoptera: Tortricidae): effects of constant daylengths and temperature on larval diapause development. Environ. Entomol. 12: 71-75.
- Rock, G.C. and Shaffer, P.L., 1983. Developmental rates of codling moth (Lepidoptera: Olethreutidae) reared on apple at four constant temperatures. Environ. Entomol. 12: 831-834.
- Rock, G.C. and Yeargan, D.R., 1974. Flight activity and population estimates of four apple insect species as determined by pheromone traps. Environ. Entomol. 3: 508-510.
- SAS Institute Inc., 1979. SAS user's guide, 1979 edition. Raleigh, N.C. 494 pp.
- Saucier, W.J. and Bragg, A.W., 1983. Meteorological monitoring and analysis. Pp. 13-20

- in G.C. Rock and J.L. Apple (eds.), Integrated Pest and Orchard Management Systems for Apples in North Carolina. N.C. Agric. Res. Serv. Tech. Bull. 276.
- Shaffer, P.L., 1984. Mathematical structures for modeling pest populations. Biomathematics Mimeo Series No. 18, Dept. of Statistics, N.C. State Univ.
- Shaffer, P.L. and Rock, G.C., 1983. Arthropod abundance, distribution, and damage to fruit. Pp. 75-96 in G.C. Rock and J.L. Apple (eds.), Integrated Pest and Orchard Management Systems for Apples in North Carolina. N.C. Agric. Res. Serv. Tech. Bull. 276.
- Sharpe, P.J.H. and DeMichele, D.W., 1977. Reaction kinetics of poikilotherm development. J. Theor. Biol. 64: 649-670.
- Sharpe, P.J.H., Curry, G.L., DeMichele, D.W. and Cole, C.L., 1977. Distribution model of organism development times. J. Theor. Biol. 66: 21-38.
- Sharpe, P.J.H., Schoolfield, R.M. and Butler, G.D., Jr., 1981. Distribution model of *Heliothis zea* (Lepidoptera: Noctuidae) development times. Can. Entomol. 113: 845-856.
- Stamper, J.H., Nigg, H.N. and Allen, J.C., 1979. Organophosphate insecticide disappearance from leaf surfaces: an alternative to first-order kinetics. Environ. Sci. Technol. 13: 1402-1405.
- Stinner, R.E., Gutierrez, A.P. and Butler, G.D., Jr., 1974a. An algorithm for temperature-dependent growth rate simulation. Can. Entomol. 106: 519-524.
- Stinner, R.E., Rabb, R.L. and Bradley, J.R., 1974b. Population dynamics of *Heliothis zea* (Boddie) and *H. virescens* (F.) in North Carolina: a simulation model. Environ. Entomol. 3: 163-168.
- Stinner, R.E., Butler, G.D., Jr., Bacheler, J.S. and Tuttle, C., 1975. Simulation of temperature-dependent development in population dynamics models. Can. Entomol. 107: 1167-1174.
- Suski, Z.W., Labanowski, G.S. and Nowakowski, Z., 1981. Dispersal of laboratory-reared codling moth males, *Laspeyresia pomonella* (L.) in central Poland. Ekol. Polska 29: 441-449.
- Sutton, T.B., Shaffer, P.L., Rock, G.C., Nardacci, J.F. and Klimstra, D.E., 1983. Fungicide, insecticide and miticide use patterns. Pp. 67-74 in G.C. Rock and J.L. Apple (eds.), Integrated Pest and Orchard Management Systems for Apples in North Carolina. N.C. Agric. Res. Serv. Tech. Bull. 276.
- Tadic, M., 1963. The biology of the codling moth (*Carpocapsa pomonella* L.) as the basis for its control. U.S. Dept. of Commerce, Office of Technical Services OTS 60-21681, 97 pp. [Translation of 1957 paper, Univ. of Belgrade]
- Taylor, F., 1981. Ecology and evolution of physiological time in insects. Am. Nat. 117: 1-23.
- Thorpe, M.R., 1974. Radiant heating of apples. J. Appl. Ecol. 11: 777-760.
- Trottier, R. and Hagley, E.A.C., 1979. Influence of temperature and snowfall on codling moth fecundity. Environ. Entomol. 8: 1052-1054.
- Tukey, J.W., 1977. Exploratory data analysis. Addison-Wesley Publ. Co., Reading, Mass. 688 pp.
- University of Rhode Island, 1968. Pesticide residue investigations on raw agricultural

- commodities. Univ. Rhode Island Agric. Exp. Stn. Bull. 395.
- Wearing, C.H., 1979. Integrated control of apple pests in New Zealand. 10. Population dynamics of codling moth in Nelson. N.Z. J. Zool. 6: 165-199.
- Wearing, C.H. and Ferguson, A.M., 1971. Variation in the fecundity of the codling moth *Carpocapsa pomonella* L. N.Z. J. Sci. 14: 233-237.
- Westigard, P.H., Gentner, L. and Butt, B.A., 1976. Codling moth: egg and first instar mortality on pear with special reference to varietal susceptibility. Environ. Entomol. 5: 51-54.
- Williams, D.G. and McDonald, G., 1982. The duration and number of the immature stages of codling moth *Cydia pomonella* (L.) (Tortricidae: Lepidoptera). J. Austr. Entomol. Soc. 21: 1-4.
- Wood, T.G., 1965. Field observations on flight and oviposition of codling moth and mortality of eggs and first-instar larvae in an integrated control orchard. N.Z. J. Agric. Res. 8: 1043-1059.
- Welch, S.M., Croft, B.A., Brunner, J.F. and Michels, M.F., 1978. PETE: an extension phenology modeling system for management of multi-species pest complex. Environ. Entomol. 7: 482-494.
- Zavaleta, L.R., and Dixon, B.L., 1982. The economic benefits of Kalman filtering for insect pest management. J. Econ. Entomol. 75: 982-988.

APPENDIX A. MODEL PARAMETERIZATION

Developmental rate

Larvae and pupae: Data from Williams and McDonald (1982) and E. A. C. Hagley (personal communication, 1982) indicated that the developmental period for larvae represents a relatively fixed proportion of the total developmental time for larvae plus pupae (range 0.503 - 0.590), so the mean proportion (0.569) was used to estimate larval and pupal developmental periods from combined times for larvae plus pupae given by Pristavko and Degtyarev (1972) and Rock and Shaffer (1983). The Gaussian function

$$Rate = R_{\max} \cdot e^{\left(-\frac{1}{2} \left[\frac{T - T_{\max}}{T_{\sigma}} \right]^2\right)}$$

where $R_{\max}$ is the maximum rate of development, T is the temperature, $T_{\max}$ is the temperature at which $R_{\max}$ occurs, and T_{σ} is difference in temperature from $T_{\max}$ at which $Rate = 0.607R_{\max}$, was fitted to the data from the four sources mentioned by nonlinear regression. For larvae, the fitted parameters were $R_{\max} = 0.0678 \text{ day}^{-1}$, $T_{\max} = 33.2^{\circ}\text{C}$, and $T_{\sigma} = 10.8^{\circ}\text{C}$; the coefficient of determination, R^2 , was 0.93. For pupae, $R_{\max} = 0.0906 \text{ day}^{-1}$, $T_{\max} = 33.3^{\circ}\text{C}$, and $T_{\sigma} = 10.6^{\circ}\text{C}$, with $R^2 = 0.95$.

Wintering stage: Data from E. A. C. Hagley (personal communication, 1982) at five temperatures from 15 to 30°C were fitted to the Gaussian function by nonlinear regression. The limited data above $T_{\max}$ made it necessary to fix $T_{\max}$ (at 32.2°C) to force

reasonable estimates of the other parameters. The parameter estimates were $R_{\max} = 0.0386 \text{ day}^{-1}$, and $T_{\sigma} = 10.5^{\circ}\text{C}$, with $R^2 = 0.95$. Geier (1963) gives data on developmental times of wintered pupae versus mean of temperature during the developmental period, and at one controlled temperature; these developmental periods are about half of the values from Hagley. The cause of these differences is unknown.

Eggs: Developmental rate versus temperature data from Glenn (1922a) were fitted by to the Gaussian function by nonlinear regression. The parameter estimates were $R_{\max} = 0.183 \text{ day}^{-1}$, $T_{\max} = 29.8^{\circ}\text{C}$, and $T_{\sigma} = 9.8^{\circ}\text{C}$, with $R^2 = 0.999$.

Searching stage: A quadratic function was parameterized from estimates of the lower threshold, T_{low} (below which the function has a value of zero), the upper threshold, T_{high} (at and above which the function equals zero), and $R_{\max}$, the maximum rate. Based on larval movement (Jackson, 1982), T_{low} was estimated to be 10°C , and T_{high} was estimated as 45°C . Maximum rate was estimated as the inverse of mean total time taken by larvae to find and penetrate fruits, 155 minutes or 0.108 day (Hall, 1934), giving $R_{\max} = 9.29 \text{ day}^{-1}$.

Adult longevity: Data from Hagley (1972) were fitted to a modified logistic function of the form

$$\text{Rate} = R_{\min} + \frac{R_{\max} - R_{\min}}{1 + \exp(a - bT)},$$

where *Rate* is the inverse of longevity (day^{-1}), $R_{\min}$ is the minimum rate, $R_{\max}$ is the maximum rate, and a and b affect location and slope of the inflection point of the function. $R_{\min}$ and $R_{\max}$ values were estimated by eye to be 0.015 and 0.080 day^{-1} , respectively, and a and b were determined by nonlinear regression to be 5.17 and $0.221^{\circ}\text{C}^{-1}$ respectively, with $R^2 = 0.995$. Pristavko and Degtyarev (1972) also give values for adult longevity, but these values are quite erratic, and so were not used.

Total production

Egg survival: The quadratic function was fitted to the data in Hagley (1972) by linear regression ($R^2 = 0.98$). The parameters estimates were: lower threshold of 10.8°C , upper threshold of 36.3°C , and maximum survival of 87.4%.

Larval survival: Lower and upper survival limits were estimated to be 18.3 and 35.0°C , based on data for larvae and pupae together (Pristavko and Degtyarev, 1972). To determine maximum survivorship, values from all relevant studies were combined to determine the mean and range of survival. For larvae in apples, mean survival (under field conditions or with only a single larva per apple) was 66%, with a range of 55 to 85% (Ferro et al., 1975; Geier and Briese, 1978; Wearing, 1979). On this basis, maximum survival was set at 70% in the quadratic function.

Searching larval survival: The same values for lower and upper thresholds as used for larvae were used for searching larvae. Reports on survival of first instar larvae indicate a mean survival rate of 51%, with a range of 24 to 90% (Hall, 1934; MacLellan, 1962; MacLellan, 1963; Wood, 1965; Ferro et al., 1975; Westigard et al., 1976; Geier and Briese,

1978; Wearing, 1979). The maximum survival was set at 60% in the quadratic function.

Pupal survival: Lower and upper thermal limits were estimated from the data in Proverbs and Newton (1962) to be 16.9 and 30.8°C. Mortality of the larvae between leaving the host fruit and pupation was included with mortality of pupae, as the transition from larva to pupa is not observable within the cocoon spun by the larva. Survival of non-diapausing 5th instar larvae after leaving the apple has been estimated at between 67 and 95%, with a mean of 77% across reports (Garlick, 1948; Ferro et al., 1975; Geier and Briese, 1978). Survival of pupae has been found to range between 87 and 98%, with a mean of 94% (Proverbs and Newton, 1962; Hathaway et al., 1971; Ferro et al., 1975; Geier and Briese, 1978). Maximum survival of the pupal stage (including larvae that have left the apple) was set at 70% in the quadratic function of survival versus temperature.

Adult oviposition: Sex ratios have been reported to vary within years (Hall, 1929; Hagley, 1974; Riedl et al., 1976), among years (MacLellan, 1972; Glen et al., 1981), and between strains (Geier and Briese, 1978) and sites (Riedl et al., 1976), but these ranges of ratios reported generally bracket 1. Thus, a sex ratio of one was assumed for the purposes of computing egg production per individual. The lower thermal threshold of oviposition was estimated to be 15.6°C (Putman, 1963), and the upper thermal threshold was estimated as 32.2°C (Isley, 1938; Klinger et al., 1958). Fecundity reported for codling moths has varied tremendously, both within and among studies (Geier, 1963; Putman, 1963; Deseo, 1971; Wearing, 1979). Fecundities from these and other reports (Hough et al., 1926; Hough, 1943; Proverbs and Newton, 1962; Gehring and Madsen, 1963; Tadic, 1963; Hathaway et al., 1971; Howell, 1971; Wearing and Ferguson, 1971; Hagley, 1972; Howell, 1972; Deseo, 1973; Hagley, 1973; Hathaway et al., 1973; Hagley, 1974; Ferro et al., 1975; Geier and Briese, 1978; Trottier and Hagley, 1979; Riedl and Loher, 1980; Brown and Brown, 1982) were tallied; average fecundity ranged from 24 to 208 eggs per female, and the overall mean was about 88 eggs per female. Since these values were obtained at a range of constant and fluctuating temperatures, a fecundity of 100 eggs per female at the optimum temperature was used in the model. Taking into account the sex ratio, the maximum of the production function for adults was 50 eggs per individual.

Cumulative production

Immature transition: Because age of immatures is defined such that cumulative production equals 0.5 at age equal to 1, the location of the function $y = \exp[-\exp(a - bt)]$ (Dobie, 1978) is fixed, and only a single parameter is left to be fitted to the data. The parameter b can be determined from the slope of the cumulative emergence curve at the median development time, as $b = (2/\ln 2)\delta y/\delta t$; it follows then that $a = b + \ln(\ln 2)$. Developmental times of codling moth immatures (larval plus pupal period) from the data sets used by Rock and Shaffer (1983) were used to form the empirical cumulative distribution functions for emergence at four temperatures. These distributions were normalized to have a mean of 1 in the manner of Sharpe et al. (1981); the normalized distributions had very similar shapes, supporting the same-shape assumption. The slope of the normalized data at $y = 0.5$ was then determined to be 2.62, giving $b = 7.55$, and $a = 7.18$. This same function was used for all immature stages, as no data were available

for the other stages.

Adult reproduction: Data on the distribution of reproduction versus age was obtained from individual records of moth oviposition and lifespan (Glenn, 1922b), and from graphs of cumulative oviposition and survivorship versus degree days for three cohorts (Geier and Briese, 1978). The records from Glenn (1922b) were used to compute cumulative oviposition versus fraction of adult life. Age of 50% oviposition was estimated as 0.30, and slope at this age was 1.89. The oviposition curves given by Geier and Briese (1978) were scaled so that age equalled 1 at the degree-day when 50% of the cohort was alive. The age of 50% cumulative oviposition was determined, and the slope at this point was measured for each cohort. The average of three values was then taken for age of 50% oviposition and slope at this age. Mean age of oviposition was larger (0.46) than from the Glenn (1922b) data, but the slope was very similar (1.94). The average values of age of 50% reproduction (0.38) and slope at this age (1.92) over the two sources were used in the model, giving parameter values of $b = 5.55$ and $a = 1.74$ in Dobie's (1978) function.

Cumulative loss

Immature loss: Due to lack of data, this was assumed to be identical with the cumulative production function for all immature stages.

Adult mortality: Since age of adults in the model is defined to be 1 at 50% survival, the two parameters of the logistic equation become equal, so that

$$y = \frac{1}{1 + \exp(a - at)},$$

where y is the cumulative mortality, t is age, and a equals 4 times the slope at the point of 50% mortality. The cumulative loss function actually used in the model was modified slightly so that the function equals 0 at age 0; the equation is

$$y = \frac{1 + \exp(a)}{1 + \exp(a - at)} - \exp(a).$$

The slope of the cumulative mortality curves given by Howell (1981) was estimated to be 0.75, so $a = 3.0$.

APPENDIX B. PESTICIDE PARAMETERIZATION

The parameters for the relationship of application rate to residue, the degradation rate of the residue, and the probit mortality-log residue function were obtained from the literature, estimated by regression on published data, or approximated as being similar to other pesticides for all of the insecticides (Table B1) which were used in the commercial orchards used for model evaluation (Sutton et al., 1983).

Application rate - residue relationship

While most reports present residue data in units of $\mu\text{g}\cdot\text{cm}^{-2}$, some have given residue values on foliage in units of $\mu\text{g}\cdot\text{g}^{-1}$. Residue values given in units of $\mu\text{g}\cdot\text{g}^{-1}$ were converted to $\mu\text{g}\cdot\text{cm}^{-2}$ using a constant of $44\text{ cm}^2\cdot\text{g}^{-1}$; this value (roughly the inverse of areal

leaf density) was determined as the slope of a linear regression passing the origin on data giving residue of two pesticides measured in both ways (McEwen et al., 1980). A linear regression through the origin was done on all available data on pesticide application rate, in units of kg active ingredient (a.i.) per ha, and resulting residue (Madsen and Williams, 1968; McMechan et al., 1972; Hameed and Allen, 1976; Pree et al., 1976; Chiba et al., 1978; Menzies et al., 1979; Hagley and Chiba, 1980; McEwen et al., 1980). The slope of this regression, and thus the conversion factor from $\text{kg}\cdot\text{ha}^{-1}$ a.i. to $\mu\text{g}\cdot\text{cm}^{-2}$, was 2.21 (S.E. ± 0.15); the R^2 of the regression was 0.53. This factor was used to convert all pesticide application rates to initial residue on leaves for mortality estimation.

Degradation rates

For each of the pesticides used (Table B1), we attempted to find published decay rates of residues on apple foliage or data on levels of residues on apple leaves with time after application. When such data were found, the decay rate was estimated as the slope of a linear regression through the origin of log (fraction of original residue) versus time. Sources of data, by insecticide, were: azinphosmethyl: Madsen and Williams (1968), Pree et al. (1976); carbaryl: Gratwick and Tew (1966); dimecron: Gratwick and Tew (1966); dimethoate: Pree et al. (1976); endosulfan: Chiba et al. (1978); malathion: Gratwick and Tew (1966); parathion: McEwen et al. (1980); phosalone: Hameed and Allen (1976), McEwen et al. (1980); prolate: Univ. Rhode Island (1968). The decay rate for demeton was guessed to be similar to that of dimethoate, and the decay rate of methomyl was guessed as similar to that of prolate. Values used for decay rates in the model are given in Table B1.

Residue-mortality relationship

The function used to compute mortality resulting from a residue level, R , was:

$$\text{mortality} = \text{probnorm} \left[b \log \left(\frac{R}{LR_{50}} \right) \right]$$

where $\text{probnorm}(u)$ is the probability that a random variable with a Normal(0, 1) distribution has a value below u , LR_{50} is the residue which results in mortality in 50% of a population, and b is the slope of the probit mortality-log residue line. Values for LR_{50} were obtained from the literature, and the value of b were obtained from the literature or computed from published LR_{50} and LR_{90} (lethal residue for 90% of population) values. Data sources, by insecticide, were: azinphosmethyl: Hameed and Allen (1976); carbaryl: Gratwick et al. (1965); demeton: guessed to be same as dimethoate; dimecron: Gratwick and Tew (1966); dimethoate: Gratwick and Tew (1966); endosulfan: Gratwick (1964); malathion: Gratwick and Tew (1966); methomyl: guessed to be similar to azinphosmethyl; parathion: Gratwick et al. (1965), Gratwick and Tew (1966); phosalone: Hameed and Allen (1976); prolate: guessed to be intermediate between azinphosmethyl and malathion. Values of LR_{50} and b used in the computation of larval survivorship are given in Table B1.

APPENDIX C. PASCAL SOURCE CODE FOR SIMULATION PROGRAM

```

PROGRAM MODELA (PESTFILE,WTHRFILE,OUTPUT,SURVFILE);
{BASIC MODEL WHICH PRODUCES PRINTED OUTPUT OF ALL STAGES}
CONST
  MAXLONG = 20; {LENGTH OF A LONG NAME}
  MAXSHORT = 10; {LENGTH OF A SHORT NAME}
  MAXSTAGE = 8; {MAXIMUM NUMBER OF STAGES}
  MIN = 1.0E-06; {MINIMUM VALUE TO RETAIN OR ADD A COHORT}
TYPE
  LONGNAME = STRING(MAXLONG);
  SHORTNAME = STRING(MAXSHORT);
  COHORTPTR = @COHORT;
  COHORT = RECORD
    N,           {NUMBER IN COHORT}
    AGE,         {PHYSIOLOGICAL AGE = MATURITY}
    F,           {CUMULATIVE MORTALITY AT AGE}
    P: REAL;     {CUMULATIVE PRODUCTION AT AGE}
    NEXT: COHORTPTR; {LINK TO NEXT COHORT}
  END;
  STAGEREC = RECORD
    NAME: SHORTNAME;
    NEXTSTAGE: INTEGER; {STAGE PRODUCED BY THIS STAGE}
    FIRST: COHORTPTR; {BEGINNING OF LINKED LIST OF COHORTS}
    DELTAAGE,      {CHANGE IN AGE IN ONE DAY}
    LEVEL,         {MEAN PRODUCTION LEVEL FOR ONE DAY}
    NEWNUM,        {NUMBER OF NEXTSTAGE PRODUCED IN ONE DAY}
    TOTNUM: REAL;  {TOTAL NUMBER IN STAGE}
    NUMCOH: INTEGER; {CURRENT NUMBER OF COHORTS}
    SURVIVAL: REAL; {DAILY EXOGENOUS SURVIVAL, E.G. PESTICIDE EFFECT}
  END;
VAR
  PTR, LASTPTR: COHORTPTR;
  STAGE: ARRAY [1..MAXSTAGE] OF STAGEREC;
  NUMSTAGES: INTEGER;           {ACTUAL NUMBER OF STAGES}
  ICURR, I, DAY, HOUR: INTEGER;
  N, AGE, F, P: REAL;           {SAME AS IN STAGEREC}
  RATESUM, TOTSUM, TMP: REAL;   {USED IN WITHIN-DAY INTEGRATION}
  PSUM: REAL;                   {SUMMATION OF PRODUCTION OVER COHORTS}
  NEXTAGE, NEXTF, NEXTP, NADJ: REAL; {TEMPORARY COHORT VARIABLES}
  TEMP: ARRAY [0..23] OF REAL; {HOURLY TEMPERATURES}
  PESTFILE, WTHRFILE: TEXT;     {INPUT DATA FILES}
  PESTNAME, WEATHERNAME: LONGNAME;
  SURVFILE: TEXT;               {FILE OF DAILY SURVIVORSHIPS FOR SEARCHING LARVAE}
  SURVDAY: INTEGER;             {CURRENT DAY ACCESSED IN SURVFILE}
  TOTALLARVAE: REAL; {TOTAL NUMBER OF INDIVIDUALS ENTERING LARVAL STAGE}
  SURVNAME: LONGNAME;           {HEADER OF SURVIVAL FILE}
  NUMHOURS: INTEGER;

```

```
PROCEDURE NEWCOHORT (VAR FIRST: COHORTPTR; NEWN, NEWAGE, NEWF, NEWP: REAL);
{INSERTS A NEW COHORT AT THE HEAD OF THE LIST POINTED TO BY FIRST}
```

```
VAR
```

```
    PTR: COHORTPTR;
```

```
BEGIN
```

```
    NEW(PTR);
```

```
    WITH PTR@ DO
```

```
    BEGIN
```

```
        NEXT := FIRST;
```

```
        N := NEWN;
```

```
        AGE := NEWAGE;
```

```
        F := NEWF;
```

```
        P := NEWP;
```

```
    END;
```

```
    FIRST := PTR;
```

```
END; {NEWCOHORT}
```

```
FUNCTION EXPCK (X: REAL): REAL;
```

```
CONST MIN = -100.0;
```

```
BEGIN
```

```
    IF X < MIN THEN EXPCK := 0.0
```

```
    ELSE EXPCK := EXP(X);
```

```
END; {EXPCK}
```

```
FUNCTION PRODUCE (STAGE: INTEGER; AGE: REAL): REAL;
```

```
{CUMULATIVE PRODUCTION FUNCTION OF STAGE TO NEXTSTAGE[STAGE] AT AGE  
= EMERGENCE OR REPRODUCTION, SCALED BY LEVEL}
```

```
VAR F: REAL;
```

```
BEGIN
```

```
    IF STAGE < 6 THEN {IMMATURE - TRANSITION}
```

```
        F := 7.1835 - 7.55*AGE
```

```
    ELSE {ADULT - REPRODUCTION}
```

```
        F := 1.70225 - 5.444*AGE;
```

```
    IF F > 3.0 THEN PRODUCE := 0.0
```

```
    ELSE IF F < -20.0 THEN PRODUCE := 1.0
```

```
    ELSE PRODUCE := EXPCK(-EXP(F));
```

```
END; {PRODUCE}
```

```
FUNCTION LOSS (STAGE: INTEGER; AGE: REAL): REAL;
```

```
{CUMULATIVE LOSS FUNCTION FROM STAGE AT AGE = MORTALITY +  
TRANSITION TO NEXT STAGE (IF NOT ADULT)}
```

```
CONST
```

```
    A = 3.0;
```

```
    DELTA = 0.0474258732; {1/(1+EXP(A))}
```

```
BEGIN
```

```
    IF STAGE < 6 THEN {IMMATURE} LOSS := PRODUCE (STAGE, AGE)
```

```
    ELSE {ADULT} LOSS := ((1.0+DELTA)/(1+EXP(A - A*AGE))) - DELTA;
```

```
END; {LOSS}
```

```

FUNCTION RATE (STAGE: INTEGER; TEMP: REAL): REAL;
{COMPUTE THE RATE OF DEVELOPMENT = D(AGE)/DT FOR STAGE AT TEMP}
VAR
  DRATE: REAL;

```

```

FUNCTION GAUSS (RM, TSIG, TM: REAL): REAL;
BEGIN
  GAUSS := RM*EXPCK(-0.5*SQR((TEMP - TM)/TSIG))
END;

```

```

BEGIN {RATE}
  CASE STAGE OF
    1: {OW PUPA} DRATE := GAUSS (0.039, 19.0, 90.0);
    2: {EGG} DRATE := GAUSS (0.181, 16.0, 84.0);
    3: {SEARCH} DRATE := -52.898 + 1.526*TEMP - 0.009363*SQR(TEMP);
    4: {LARVA} DRATE := GAUSS (0.061, 18.0, 87.5);
    5: {PUPA} DRATE := GAUSS (0.081, 17.0, 87.5);
    6: {ADULT} DRATE := 0.015 + 0.065/(1 + EXP(9.095 - 0.1228*TEMP));
  END;
  IF DRATE < 0.0 THEN RATE := 0.0 ELSE RATE := DRATE;
END; {RATE}

```

```

FUNCTION TOTAL (STAGE: INTEGER; TEMP: REAL): REAL;
{COMPUTE THE TOTAL PRODUCTION EXPECTED FROM STAGE I AT TEMP
- FOR ADULTS THIS EQUALS TOTAL REPRODUCTION
- FOR IMMATURE STAGES, THIS REPRESENTS TOTAL EMERGENCE TO NEXTSTAGE}
VAR
  TOT: REAL;
BEGIN
  CASE STAGE OF
    1: {OW PUPA} TOT := 1.0;
    2: {EGG} TOT := -8.2958 + 0.24672*TEMP - 0.0016595*SQR(TEMP);
    3: {SEARCH} TOT := -3.6667 + 0.1067*TEMP - 0.0006667*SQR(TEMP);
    4: {LARVA} TOT := -4.2778 + 0.1244*TEMP - 0.0007777*SQR(TEMP);
    5: {PUPA} TOT := -5.60 + 0.168*TEMP - 0.00112*SQR(TEMP);
    6: {ADULT - OVIP} TOT := -1200.0 + 33.33*TEMP - 0.2222*SQR(TEMP);
  END;
  IF TOT < 0.0 THEN TOTAL := 0.0
  ELSE TOTAL := TOT;
END; {TOTAL}

```

```

FUNCTION ANOTHER (VAR ICURR: INTEGER): BOOLEAN;
{RETURNS TRUE IF THERE IS ANOTHER COHORT TO BE READ FOR STAGE ICURR}
VAR
  I: INTEGER;
BEGIN
  IF EOF(PESTFILE) THEN ANOTHER := FALSE
  ELSE
    BEGIN

```

```

        I := ICURR;
        READ (PESTFILE, ICURR);
        ANOTHER := (I = ICURR);
    END;
END; {ANOTHER}

PROCEDURE GETSURVIVAL (DAY: INTEGER);
{FILL SURVIVAL ARRAY FROM SURVFILE -
  USES GLOBAL VARIABLES SURVFILE, STAGE, AND SURVDAY }
VAR
    I: INTEGER;
BEGIN
    FOR I := 1 TO NUMSTAGES DO WITH STAGE[I] DO
        IF I <> 3 THEN SURVIVAL := 1.0
        ELSE
            BEGIN {SEARCHING LARVA}
                WHILE SURVDAY < DAY DO
                    BEGIN
                        READLN (SURVFILE); {SKIP TO NEXT RECORD IN FILE}
                        IF EOF(SURVFILE) THEN SURVDAY := MAXINT {TO PREVENT FURTHER READS}
                        ELSE READ (SURVFILE, SURVDAY);
                    END;
                IF DAY = SURVDAY THEN READ (SURVFILE, SURVIVAL)
                ELSE SURVIVAL := 1.0; {IF DAY < SURVDAY}
            END; {SEARCHING LARVA}
        END; {GETSURVIVAL}
    END;

PROCEDURE GETCOHORTS;
BEGIN
    READLN (PESTFILE, PESTNAME);
    NUMSTAGES := 0;
    READ (PESTFILE, I);
    WHILE NOT EOF(PESTFILE) DO WITH STAGE[I] DO
        BEGIN
            READ (PESTFILE, NEXTSTAGE);
            READLN (PESTFILE, NAME);
            NUMSTAGES := NUMSTAGES + 1;
            FIRST := NIL;
            WHILE ANOTHER (I) DO
                BEGIN
                    READLN (PESTFILE, N, AGE);
                    F := LOSS (I, AGE);
                    P := PRODUCE (I, AGE);
                    NEWCOHORT (FIRST, N, AGE, F, P);
                END;
            END;
        END; {GETCOHORTS}
    END;

BEGIN {MODEL}

```

```

TOTALLARVAE := 0.0;
RESET (PESTFILE);
GETCOHORTS;
RESET (WTHRFILE);
READ (WTHRFILE, NUMHOURS, DAY); {NUMBER OF TEMPERATURES/DAY AND START DAY}
READLN (WTHRFILE, WEATHERNAME);
RESET (SURVFILE);
READLN (SURVFILE, SURVNAME); {READ SURVIVAL FILE HEADING}
WRITELN (PESTNAME, ' AT ', WEATHERNAME, ' (SURVIVAL FROM ', SURVNAME,')');
WRITE ('DAY T[6] T[15]');
FOR I := 1 TO NUMSTAGES DO WRITE (STAGE[I].NAME:15);
WRITELN;
READ (SURVFILE, SURVDAY); {GET STARTING DATE OF SURVIVAL DATA}
WHILE NOT EOF(WTHRFILE) DO
BEGIN
  FOR HOUR := 0 TO NUMHOURS - 1 DO READ (WTHRFILE, TEMP[ HOUR]);
  READLN (WTHRFILE);
  GETSURVIVAL (DAY);
  FOR I := 1 TO NUMSTAGES DO WITH STAGE[I] DO
  BEGIN
    RATESUM := 0.0;
    TOTSUM := 0.0;
    FOR HOUR := 0 TO NUMHOURS - 1 DO
    BEGIN
      TMP := TEMP[ HOUR];
      RATESUM := RATESUM + RATE(I, TMP);
      TOTSUM := TOTSUM + TOTAL(I, TMP);
    END;
    DELTAAGE := RATESUM/NUMHOURS; {DAILY INCREMENT OF MATURITY}
    LEVEL := TOTSUM/NUMHOURS; {AVERAGE SURVIVAL OR PRODUCTION LEVEL}
    NEWNUM := 0.0;
  END;
  FOR I := 1 TO NUMSTAGES DO WITH STAGE[I] DO
  BEGIN
    PSUM := 0.0; {SUM OF PRODUCTION OF NEXTSTAGE}
    TOTNUM := 0.0; {SUM OF NUMBER IN STAGE I}
    NUMCOH := 0; {NUMBER OF COHORTS IN STAGE I}
    PTR := FIRST; {START OF LINKED LIST OF COHORTS}
    LASTPTR := PTR; {TRAILS PTR FOR POSSIBLE COHORT DELETION}
    WHILE PTR <> NIL DO WITH PTR@ DO {UPDATE A COHORT}
    BEGIN
      NEXTAGE := AGE + DELTAAGE;
      NEXTP := PRODUCE (I, NEXTAGE);
      IF I<6 {IMMATURE} THEN NEXTF := NEXTP {STAGE DEPENDENT TO }
      ELSE NEXTF := LOSS (I, NEXTAGE); { SAVE COMPUTATION}
      NADJ := N * SURVIVAL / (1.0 - F);
      PSUM := PSUM + NADJ*(NEXTP - P);
      N := NADJ * (1.0 - NEXTF);
      IF N < MIN THEN {DELETE COHORT}

```

```

BEGIN
  IF PTR = FIRST THEN FIRST := NEXT
  ELSE LASTPTR@.NEXT := NEXT; {DON'T CHANGE LASTPTR}
  DISPOSE (PTR);
END
ELSE {UPDATE COHORT ATTRIBUTES AND TOTALS}
BEGIN
  TOTNUM := TOTNUM + N;
  NUMCOH := NUMCOH + 1;
  F := NEXTF;
  P := NEXTP;
  AGE := NEXTAGE;
  LASTPTR := PTR;
END;
PTR := NEXT;
END;
STAGE[NEXTSTAGE].NEWNUM := STAGE[NEXTSTAGE].NEWNUM + LEVEL*PSUM;
END;
FOR I := 1 TO NUMSTAGES DO WITH STAGE[I] DO
BEGIN
  IF NEWNUM >= MIN THEN {ADD A NEW COHORT TO STAGE[I]}
  BEGIN
    NEWCOHORT(FIRST, NEWNUM, 0.0, 0.0, 0.0);
    TOTNUM := TOTNUM + NEWNUM;
    NUMCOH := NUMCOH + 1;
  END;
END;
END;
WRITE (DAY: 3, TEMP[6]:6:1, TEMP[15]:6:1);
FOR I := 1 TO NUMSTAGES DO WITH STAGE[I] DO
  WRITE (TOTNUM:10:4, NUMCOH:5);
WRITELN;
DAY := DAY + 1;
TALLARVAE := TALLARVAE + STAGE[4].NEWNUM;
END;
WRITELN ('TOTAL LARVAE = ',TALLARVAE:10:2);
END. {MODEL A}

```

APPENDIX D. IMPLEMENTATION OF THE SIMULATION MODEL

The codling moth simulation model is written in Pascal, and should be useable on any computer with a Pascal compiler (note that Waterloo Pascal is an interpreter and the program would run extremely slowly). The Pascal source program supplied is written for the IBM VS Pascal compiler. There are only two non-standard features used: (1) all pointer references use @ instead of ^, e.g. @cohort and ptr@ instead of ^cohort and ptr^; (2) strings are used for names and labels to simplify reading. These should be easily adapted to any other Pascal compiler. Assignment of files to physical data sets is done by having the DDNAME in JCL match the filename in the program, or, for interactive use, ALLOCating files with matching names. Other Pascal compilers may require ASSIGN statements, etc.

The program uses three input files: PESTFILE, WTHRFILE, and SURVFILE.

- PESTFILE contains the basic input data consisting of insect name, stage names, number of the following stage, and initial cohort sizes and ages. The first line contains the insect name (up to 20 characters); the following lines contain data on stages (not necessarily in numerical order). Data for each stage consists of a header line with the stage number (must be ≥ 1), number of the stage which it produces (for current model: 6 for stage 1, 2 for stage 6, and $i+1$ for stage i if $2 \leq i \leq 5$), then stage name (up to 10 characters), followed by an arbitrary number of lines specifying the initial cohorts in the stage (may be none) consisting of stage number, initial number in cohort, and initial age of the cohort.
- WTHRFILE contains temperature data used to drive the model. The format of the data set is: first line contains an integer specifying the number of temperature observations per day in the file (which will be the number of iterations per day for temperature-dependent functions in the model), then an integer specifying the starting day of the weather data (which will be the starting day of the simulation), then the name of the location for the weather data (up to 20 characters); each of the following lines represent one day, and should contain the specified number of temperatures per day (may be real values, format is not important). The simulation will run for as many days as there are observations in the weather file.
- SURVFILE is a file of survivorships by day for the searching stage, produced from a record of pesticide applications. The first line of this file is a header identifying the source of the survival values (e.g. orchard and year, up to 20 characters), followed by 1 or more lines of data each containing day of the year (an integer) and the survival value (0.0 to 1.0) for that day. Note that in the current model, only stage 3, searching larvae, is affected by the survival data. To force all survival values to one, use a date larger than 366.

All program output goes the standard file OUTPUT. The output consists of two header lines followed by one line per day of the simulation. The first header line contains names (headers) from PESTFILE, WTHRFILE, and SURVFILE. The second header line labels the columns of output following. After the day, the temperature at 0600 H and at 1500 H is printed (note: this will work properly only for 24 temperature measurements per day; modify or eliminate printing of these otherwise); this is done to give an idea of

temperature range for that day. For each stage in the model, the total number of individuals and the total number of cohorts are printed; number of cohorts depends fairly strongly on the value of MIN, the minimum number in a cohort for creation or retention, but number of individuals should depend only very weakly on this constant. Thus, number of cohorts is printed as an aid in following the workings of the model. All of our analyses were based only on number of larvae and adults. The final line of the printout is the total number of individuals which entered the larval stage; this is printed separately as it cannot be determined from the numbers presently in the stages.

The tape contains five files:

- (1) MODEL.PASCAL, the model source in Pascal.
- (2) WEATHER.DATA, a sample input weather file.
- (3) SURVIVAL.DATA, a sample input survival file.
- (4) PEST.DATA, the basic data with a single initial cohort of 100 individuals of age 0 in the wintering stage.
- (5) MODEL.OUTPUT, the output of the model using the input files listed above.

APPENDIX E. RUNNING THE SIMULATION MODEL

There are five versions of the model which differ in data input requirements and output production, but are identical mathematically. Associated with each version are files of JCL needed to run these programs; these files are all stored as members of the partitioned dataset LIB.CNTL, which will be described in more detail below. To run one of these programs in the batch stream from TSO, type SUB LIB.CNTL(member), where member is the appropriate member name, or if it needs to be modified before submission, QED LIB.CNTL(member), modify it, then SUB, and SAVE if desired. Also associated with the programs are several input, intermediate, and output datasets:

- LIB.DATA, a partitioned data set with members:
  - * CODMODEL contains the basic input data for 'pestfile', consisting of insect name, stage names, number of the following stage, and initial cohort sizes and ages. The first line contains the insect name (up to 20 characters); the following lines contain data on stages (not necessarily in numerical order). Data for each stage consists of a header line with the stage number (must be ≥ 1), number of the stage which it produces (for current model: 6 for stage 1, 2 for stage 6, and $i+1$ for stage i if $2 \leq i \leq 5$), then stage name (up to 10 characters), followed by an arbitrary number of lines specifying the initial cohorts in the stage (may be none) consisting of stage number, initial number in cohort, and initial age of the cohort.
  - * PARAMS contains parameters for those versions of the model (MODELS, MODEL T) that read in function coefficients as data, as for sensitivity analysis. The first number is the orchard block, and coefficients follow in order; number of coefficients per line is not important, but there should be 40 coefficients (note: coefficient 0 is not actually used, but is calculated from coefficient 1).
  - * AVL1974, AVL1975, AVL1976, AVL1977, AVL1978, AVL1979, and AVL1980 contain hourly or three-hourly (1979 and 1980) temperature data from the Asheville airport, for use as input to the model; note that the appropriate member must be specified in JCL to obtain the weather data for the desired year. The format of these data sets is: first line contains an integer specifying the number of temperature observations per day in the file (which will be the number of iterations per day for temperature-dependent functions in the model), then an integer specifying the starting day of the weather data (which will be the starting day of the simulation), then the name of the location for the weather data (up to 20 characters); each of the following lines represent one day, and contain the specified number of temperatures per day (may be real values, format is not important). The simulation will run for as many days as there are observations in the weather file.
  - * TRANWTHR contains intercepts and slopes need to convert Asheville weather data to appropriate values for each orchard block; format is one line per block, containing block number, intercept, then slope of the linear regression relating the orchard temperatures to Asheville temperatures.
  - * TOXICITY contains data on pesticide toxicity and degradation rates, arranged by code number as used in the IPOMS project, for use by the program PESTCIDE to

compute survival. The format is one line per insecticide, containing code number, concentration (fraction of the formulation that is active ingredient), decay rate (per day), lethal residue for 50% of searching larvae, and slope of the probit-log residue regression.

- * M76, M77, M78, M79, and M80 contain insecticide application records (block, date, code, and rate in lbs. or pts. per acre) for the IPOMS blocks, for use by PESTCIDE to compute survival; the appropriate member must be specified for the desired year.
- SURVIVAL.DATA is a file of survivorships by day for the searching stage, produced by the program PESTCIDE and used as input to the simulation model. In the current model, only stage 3, searching larvae, is affected by the survival data. For MODELA, MODEL P, or MODEL C, the first line of this file is a header identifying the source of the survival values (e.g. block and year, up to 20 characters), followed by 1 or more lines of data each containing day of the year (an integer) and the survival value (0.0 to 1.0) for that day; to force survivals to 1, give a day > 366. For MODEL T and MODEL S, there should be no header line, and no days > 366; to force all survivals to 1, have an empty file, or one line with two ones on it.
- MODLOUT.DATA is used for output of actual numbers of individuals in the larval and adult stages in the model, and is used as input by the programs MAXIMA, which determines occurrence of maxima in the model output for these stages, and PLOT which produces a printplot of their numbers versus date. The first line is a header identifying the block and year of the simulation run; the remaining lines contain day of the year, number of larvae, and number of adults.
- MODEL.OUT is used for output of the programs MAXIMA and PLOT (this output could be routed directly to printer with SYSOUT=* on the DD statement).

Source files for the five versions of the model, and the programs PESTCIDE, MAXIMA, and PLOT are contained as members of the partitioned dataset LIB.PASCAL.

Executable versions of all programs are kept as members of the same name in the partitioned dataset LIB.LOAD, which is used as a JOBLIB in all JCL files.

The five versions of the model and their associated JCL datasets (in LIB.CNTL) are:

- (1) MODELA is the basic version of the model, with coefficients fixed, and produces printed output of all stages; it uses the weather file directly (no transformations), and uses the survival file. This is the "export" version of the model. Associated with it are:
  - MODELAC compiles and links the program to produce an executable file;
  - MODEL AG executes the program, and produces printed output of numbers versus time, with descriptive headers.
- (2) MODEL P has coefficients fixed, uses the survival file for pesticide effects, and uses TRANWTHR to transform weather data from ASHEVILLE values to appropriate values for each orchard block. Its JCL files are:
  - PESTCIDE generates the survival file from one of the pesticide application record files (M76, M77, M78, M79, or M80) and TOXICITY data files; the

- correct year must be specified for the pesticide record file;
- MODELPC compiles and links the program;
  - MODELPS executes the program and produces a spooled SASGRAPH plot of larval and adult numbers for the Tektronics 4662A plotter;
  - MODELPG executes, then runs MAXIMA and PLOT to produce a printplot;
  - MODELPN executes with no pesticide effects (a dummy survival file), then runs MAXIMA and PLOT;
  - MODELPB runs PESTCIDE to create a survival file, then executes MODEL with this file and runs MAXIMA and PLOT, then executes MODEL with a dummy file (no pesticides) and runs MAXIMA and PLOT (for comparison of results with and without pesticides).
- (3) MODEL reads coefficients as data; the coefficients it uses are the same as used in MODELA and MODEL. Its associated JCL files are:
- MODELCC compiles and links the program;
  - MODELCG executes MODEL, then runs MAXIMA and PLOT; coefficient data are read 'inline' from this dataset.
- (4) MODEL reads coefficients as data, and reads a list of coefficients for which sensitivity analysis should be performed. Note that in MODEL and in MODELS (below) coefficients for the quadratic functions (total production and searching development rate) are in the form of Tmax, Rmax, and Tsig, i.e. location of the x-axis, maximum height, and half-width at x-intercepts, rather than as normal quadratic coefficients; the parameters as read are converted to quadratic coefficients by the procedure QUADRATIC. For each coefficient read, the value is increased by 10%, the simulation is run and maxima computed (within the same program), then the value is decreased by 10%, and the run repeated. Associated JCL files are:
- MODELTC compiles and links the program;
  - MODELTG executes the program; coefficients are read from LIB.DATA(PARAMS), and the list of coefficients are read from an execution time per coefficient tested.
- (5) MODELS produces a standard run for sensitivity analysis, with print plot output as well as the maxima that MODELCTG produces. Associated JCL files are:
- MODELSC compiles and links the program;
  - MODELSG executes the program with no coefficients altered then runs PLOT.

Table 1. Comparison of dates of peaks in adult numbers between pheromone trap records in an orchard and simulation runs based on temperatures in that orchard, with no pesticide mortality applied.

Orchard number	Year	Total trapped	First Peak		Second Peak		Third Peak	
			actual	simulated	actual	simulated	actual	simulated
32	1976	175	117	128	166	227	251	282
36	1976	216	117	123	166	230	258	282
13	1977	107	129	127	206	207	242†	275
32	1977	285	129	128	206	208	242	275
36	1977	263	129	128	206†	212	242	275
13	1978	108	142	139	205	214	‡	278
26	1978	102	142	133	212	216	§	278
32	1978	176	149	142	212	219	§	278
36	1978	256	156	142	219	222	256	286
36	1979	246	136	133	190†	221	254	296
36	1980	154	147	135	238	211	267†	270
49	1980	97	133	135	224	207	#	270

† Small peaks obscured by smoothing process.

‡ No third peak observed; last sample taken on day 240.

§ No third peak observed; last sample taken on day 256.

No third peak observed; last sample taken on day 259.

Table 2. Sensitivity of three measures of model output to changes in model parameters; see text and Appendix A for description of parameters.

Function	Stage	Parameter	Total Larvae		Larval Peak		Adult Peak	
			average	nonlin	average	nonlin	average	nonlin
Cumulative production, P_i	Immature	b	3.35	-0.26	0.0	0.0	-0.5	0.5
	Adult	a	-0.10	-0.00	0.0	0.0	0.0	0.0
		b	1.25	-0.22	-0.5	0.5	0.0	0.0
Cumulative loss, F_i	Adult	b	0.00	0.00	0.0	0.0	0.0	0.0
Developmental rate, r_i	Wintering	R_{max}	-10.07	-3.82	-3.0	-1.0	-1.5	-0.5
		T_{sig}	-15.77	-19.95	-10.0	-1.0	-8.0	3.0
		T_{max}	2.94	-64.72	31.0	6.0	19.0	-7.0
	Egg	R_{max}	3.04	-0.73	-1.0	0.0	-0.5	0.5
		T_{sig}	1.64	-0.92	-1.0	0.0	-0.5	0.5
		T_{max}	-17.61	-15.31	4.0	1.0	4.5	3.5
	Searching	T_{max}	0.00	0.00	0.0	0.0	0.0	0.0
		R_{max}	0.00	0.00	0.0	0.0	0.0	0.0
		T_{max}	0.00	0.00	0.0	0.0	0.0	0.0
	Larva	R_{max}	6.75	-1.19	-1.5	-0.5	-1.0	0.0
		T_{sig}	7.26	-1.84	-2.0	0.0	-1.0	0.0
		T_{max}	-34.83	-21.50	10.5	1.5	20.5	10.5
	Pupa	R_{max}	5.26	-0.76	0.0	0.0	-1.0	0.0
		T_{sig}	6.25	-1.42	0.0	0.0	-1.0	0.0
		T_{max}	-31.59	-17.70	0.0	0.0	11.0	4.0
	Adult	R_{min}	0.17	-0.02	0.0	0.0	-0.5	0.5
		R_{max}	1.06	-0.09	0.0	0.0	-0.5	0.5
		a	-4.41	-2.06	1.0	0.0	1.5	-0.5
		b	4.67	-1.80	-1.0	0.0	-1.5	-0.5
		T_{max}	-31.05	-14.21	1.0	0.0	0.0	0.0
Total production, c_i	Egg	R_{max}	17.25	0.72	0.0	0.0	0.0	0.0
		T_{sig}	7.17	-0.63	0.0	0.0	0.0	0.0
		T_{max}	-43.81	-6.96	0.5	-0.5	0.0	0.0
	Searching	R_{max}	17.25	0.72	0.0	0.0	0.0	0.0
		T_{sig}	10.09	-0.89	0.0	0.0	0.0	0.0
		T_{max}	-13.24	-5.89	0.0	0.0	0.0	0.0
	Larva	R_{max}	7.25	-0.00	0.0	0.0	0.0	0.0
		T_{sig}	2.88	-0.42	0.0	0.0	0.0	0.0
		T_{max}	-12.45	-7.12	0.0	0.0	0.0	0.0
	Pupa	R_{max}	7.25	-0.00	0.0	0.0	0.0	0.0
		T_{sig}	2.83	-0.39	0.0	0.0	0.0	0.0
		T_{max}	-65.21	-3.55	0.5	-0.5	0.0	0.0
	Adult	R_{max}	17.25	0.72	0.0	0.0	0.0	0.0
		T_{sig}	14.05	-0.34	0.0	0.0	0.0	0.0

Table B1. Decay rates and parameters of residue-mortality relationship for pesticides used in commercial orchards used for model evaluation.

Generic Name	Decay Rate day ⁻¹	LR ₅₀ ⁻² μg·cm ⁻²	Slope probits log ⁻¹
Azinphosmethyl	0.0896	0.079	4.10
Carbaryl	0.173	0.06	2.45
Demeton	0.125	0.30	1.83
Dimecron	0.198	0.30	2.0
Dimethoate	0.125	0.30	1.83
Endosulfan	0.265	2.15	1.03
Malathion	0.347	0.075	3.01
Methomyl	0.08	0.07	3.0
Parathion	0.372	0.02	2.13
Phosalone	0.0797	0.218	1.75
Prolate	0.0845	0.15	3.0

Figure 1. Compartmental flow diagram of the model.

Figure 2. Flow chart for computations. ▱ = inputs, ○ = output, □ = main program computations, and ▤ = process function subroutines.

Figure 3. Typical output of the simulation model showing numbers in all stages versus time, with no pesticide effects (weather data from orchard 35, 1976). Solid line is wintering stage, short dash line is eggs, medium dash line is searching stage, long dash line is larvae, short dash-medium dash line is pupae, and short dash-long dash line is adults.

Figure 4. Comparison of number of adults in simulation output without pesticide effects with smoothed number of male moths caught per trap per week in pheromone traps in the orchard from which the simulation input temperatures were obtained (orchard 36, 1978). Simulation output was scaled so the maximum value was equal to the maximum value of number of moths caught. Solid line is trap catch, and short dash line is simulation output.

Figure 5. Number of adults in a simulation run using input temperature and pesticide records from an orchard (orchard 13, 1978) where the pesticides had a moderate effect on model output, compared with smoothed numbers of moths caught in pheromone traps in that orchard, and model output without pesticide mortality. Simulation output was scaled as in Figure 4. Solid line is trap catch, short dash line is simulation with pesticides, and long dash line is simulation without pesticides.

Figure 6. Number of adults in a simulation run using input temperature and pesticide records from an orchard (orchard 26, 1978) where the pesticides had a severe effect on model output, compared with smoothed numbers of moths caught in pheromone traps in that orchard, and model output without pesticide mortality. Simulation output was scaled as in Figure 4. Solid line is trap catch, short dash line is simulation with pesticides, and long dash line is simulation without pesticides.

Figure 7. Numbers of larvae and adults in the simulation run used as the standard run for sensitivity tests when the effects of pesticides were included, with the computed survival of the searching stage resulting from pesticide residues (weather and pesticide application data were from orchard 35, 1976). Solid line is survival of the searching stage, short dash line is number of larvae, and long dash line is number of adults.