

Stochastic Phenology Model for the Western Spruce Budworm (Lepidoptera: Tortricidae)

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ABSTRACT Data were collected during 2 consecutive years on the Starkey Experimental Forest near La Grande, Oreg., to examine phenology of the western spruce budworm, *Choristoneura occidentalis* Freeman. The logistic probability distribution was used to describe distribution of budworm in each developmental stage (instar 2 through adult) as a function of accumulated degree-days by year, plot, and host species. The logistic distribution described phenology accurately and was simpler to compute than other methods. Results should interest insect-pest managers and researchers who model development of plants and animals.

TEMPERATURE-DEPENDENT insect development is important to integrated pest management. Such information on pest species is needed in nearly all management activities designed to monitor or reduce pest densities. Insect and host phenology models are central to many pest management systems.

Temperature-dependent development of insects and trees has been the subject of several studies (Read & Ashford 1968, Stinner et al. 1975, Wickman 1976, Curry et al. 1978, Birley 1979, Kemp-ton 1979, Logan et al. 1979, Regniere et al. 1981, Regniere 1982, Beckwith & Kemp 1984). Osawa et al. (1983) combined temperature-dependent development and statistical procedures in a stochastic phenology model for balsam fir, *Abies balsamea* (L.) Mill. Their results provided researchers and managers with a useful model for bud development expressed as a function of accumulated heat units.

We described an improvement to the Osawa et al. (1983) phenology model and discussed statistical procedures for parameter estimation and hypothesis testing (Dennis et al. 1986). Our objectives are to construct models that accurately describe development of western spruce budworm (*Choristoneura occidentalis* Freeman). In this paper, we apply our methods to a specific case, and describe field data, modeling methods, and results of procedures for estimating parameters.

Methods

Field Data. All data on development of western spruce budworm were collected from two plots (Bear Springs and Meadow Creek) on the Starkey Experimental Forest near La Grande, Oreg. Bear

Springs and Meadow Creek plots (ca. 5 ha each) were at elevations of 1,463 and 1,341 m. Collections were made weekly on the Bear Springs plot from 17 May through 2 August 1982 and 16 March through 17 August 1983. Weekly collections were made on the Meadow Creek plot from 16 March through 15 August 1983.

Collections both years were from 7- to 14-m Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, and grand fir, *Abies grandis* (Dougl. ex. D. Don) Lindl. In 1982, five host trees (randomly selected on each collection date) of each species were sampled on the Bear Springs plot by removing two branches from each of three crown levels (upper, middle, lower). Budworms were pooled by collection date and their developmental stages determined. In 1983, the study was expanded to two plots (addition of Meadow Creek), and samples were collected from 10 trees randomly selected by species and sample date. Samples collected from the three crown levels were pooled. Budworms collected from both plots in 1983 were separated by host species and plot. Instar was determined by measuring head-capsule width. Seven developmental stages were identified: instars 2-6, pupae, and adults.

In all, five data sets were collected, three from Bear Springs (Douglas-fir/grand fir 1982, Douglas-fir 1983, and grand fir 1983) and two from Meadow Creek (Douglas-fir 1983 and grand fir 1983).

Data on heat-unit accumulation (degree-days [DD]) above 5.5°C were collected on each plot by biophenometer during insect sampling. Accumulated DD were measured from plot establishment (yearly) until each collection date. At a given sample date, the accumulated DD were calculated as follows:

$$t = \sum_{j=1}^k \sum_{i=1}^{144} \frac{T_{ij} - T_{min}}{144}$$

subject to the restriction that

$$\text{if } T_{ij} > T_{max}, \text{ then } T_{ij} = T_{max}$$

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Table 1. Parameter estimates ($\pm 95\%$ asymptotic confidence limits) for western spruce budworm phenology models by year, plot, and host-tree species (Starkey Experimental Forest, Oregon)

Plot year (host species)	Parameters						
	a_1	a_2	a_3	a_4	a_5	a_6	b^2
Bear Springs 1982 (DF/GF) ^a	121.080 ± 8.238	204.360 ± 9.507	264.410 ± 8.478	342.473 ± 7.037	465.620 ± 4.747	599.570 ± 13.506	1.559 ± 0.265
Bear Springs 1983 (DF)	138.406 ± 17.344	189.437 ± 3.421	252.057 ± 3.036	346.688 ± 4.906	477.429 ± 12.099	601.463 ± 4.103	2.559 ± 0.253
Bear Springs 1983 (GF)	103.885 ± 2.971	163.712 ± 2.642	225.176 ± 2.034	326.325 ± 3.702	455.572 ± 7.793	587.045 ± 11.510	2.122 ± 0.132
Meadow Creek 1983 (DF)	109.843 ± 6.997	197.067 ± 3.118	271.896 ± 3.797	372.080 ± 7.290	474.112 ± 10.826	639.875 ± 20.099	3.752 ± 0.367
Meadow Creek 1983 (GF)	87.712 ± 2.765	161.693 ± 0.352	252.969 ± 4.648	378.215 ± 8.958	507.949 ± 16.501	611.233 ± 12.749	4.691 ± 0.394

^a DF, samples collected on Douglas-fir; GF, samples collected on grand fir.

where t = accumulated DD, K = number of days to present sample date from start of study, 144 = number of 10-min periods in a single day, T_{ij} = ambient air temperature sampled by biophenometer every 10 min, T_{\min} = minimum temperature required for development (5.5°C), and T_{\max} = maximum temperature where development still occurred (35.0°C).

Model. The model used to describe phenology of the western spruce budworm, summarized here, is explained in detail elsewhere (Dennis et al. 1986). Assuming that the proportion of the population in development stage i at sampling time j is given by (p_{ij}),

$$p_{ij} = 1 / \left\{ 1 + \exp \left[- \left(\frac{a_i - t_j}{\sqrt{b^2 t_j}} \right) \right] \right\} - 1 / \left\{ 1 + \exp \left[- \left(\frac{a_{i-1} - t_j}{\sqrt{b^2 t_j}} \right) \right] \right\},$$

where t_j = DD accumulated at sample time j ($j = 1, 2, \dots, q$), a_i = amount of development needed (here, DD) to complete the i th stage ($t = 1, 2, \dots, r - 1$), and b^2 = a positive constant. For any given data set, the parameters a_1, a_2, \dots, a_{r-1} , and b^2 need to be estimated using maximum likelihood procedures. For completeness, a_0 and a_r are assumed to be $-\infty$ and $+\infty$. The quantity p_{ij} represents the area under a logistic probability density curve between a_{i-1} and a_i , the logistic distribution has a mean of t_j and a variance of $(\pi^2/3)b^2 t_j$. Once the parameter estimates are computed, the estimated proportion of insects in development stage i , p_{ij} , can be plotted as a function of t_j .

For the western spruce budworm, $r = 7$ represents five instars (2-6), pupa, and adult. As DD accumulate, the logistic probability density curve moves through the a_i values, causing corresponding changes in the proportions (p_{ij}). When t_j is small, most of the insects are to be found in the early stages; as t_j increases, more insects are found in advanced stages.

Results and Discussion

The model was fit separately to each of the five western spruce budworm data sets using methods described elsewhere (Dennis et al. 1986). Maximum likelihood parameter estimates (a_i 's and b^2) for each data set are contained in Table 1.

Comparison of Model Predictions and Data. Raw data and model predictions were compared (using Table 1 parameters) by life stage (7) for each of the five models developed (Fig. 1-5). The model-estimated proportion of insects in development stage i , p_{ij} , was plotted as a function of time t_j (DD). Although models were developed using actual frequencies in each life stage by sample date, proportions were used to eliminate scale differences and improve visual comparison.

Actual data, expressed as proportions, were compared with model predictions for instars 2-6, pupae, and adults for western spruce budworms collected on Douglas-fir and grand fir on the Bear Springs plot in 1982 (Fig. 1). Model estimates conform to actual observations for each life stage. No second instars were found after ca. 240 DD. Instars 3, 4, and 5 showed peaks at ca. 160, 230, and 310 DD, respectively, and each stage was present in samples over a span of 250 DD. Instar 6 and pupae were present longer than previous stages, and each spanned nearly 350 DD. Peak densities for sixth instars and pupae were estimated at 400 and 530 DD. Model results suggested that adults were first present at around 520 DD, and the entire population was in the adult stage at 800 DD.

Raw data were compared with model predictions of western spruce budworm phenology for a population living on Douglas-fir on the Bear Springs plot in 1983 (Fig. 2). Second instars were found only before 270 DD. Instars 3, 4, and 5 on Douglas-fir were present for 230-330 DD and showed peaks at 170, 220, and 300 DD, respectively. For this data set, as with the 1982 data, sixth instars were collected over the greatest period of time (450 DD, with a peak at ca. 420 DD). The time during which pupae were found was similar to

budworm phenology models

a_6	b^2
599.570	1.559
± 13.506	± 0.265
601.463	2.559
± 4.103	± 0.253
587.045	2.122
± 11.510	± 0.132
639.875	3.752
± 20.099	± 0.367
611.233	4.691
± 12.749	± 0.394

Discussion

tely to each of the five data sets using methods (Kemp et al. 1986). Maximum estimates (a_i 's and b^2) are listed in Table 1.

Predictions and Data. Model results were compared with observed data by life stage (7) for Douglas-fir and grand fir (Fig. 1-5). The number of insects in development was plotted as a function of accumulated DD. Models were developed for each life stage by sample size to eliminate scale differences for comparison.

Model results were compared with observed proportions, were used for predictions for instars 2-6, and for western spruce budworms on Douglas-fir and grand fir on the Bear Springs plot. Model estimates compared with observed data for each life stage. No insects were collected after ca. 240 DD. Instars 2, 3, 4, and 5 were present at ca. 160, 230, and 310 DD, respectively. Instar 6 and pupae were present at ca. 390 DD, and each had peak densities for sixth instar at 400 and 530 DD. All instars and pupae that adults were first collected at 800 DD.

Model results were compared with model predictions for western spruce budworm phenology for a population of Douglas-fir on the Bear Springs plot. Instars 2 through 6 and pupae were found at 160, 230, 310, 390, 420, and 530 DD, respectively. For 1982 data, sixth instars were present for the longest period of time (ca. 420 DD). The time period for each life stage found was similar to

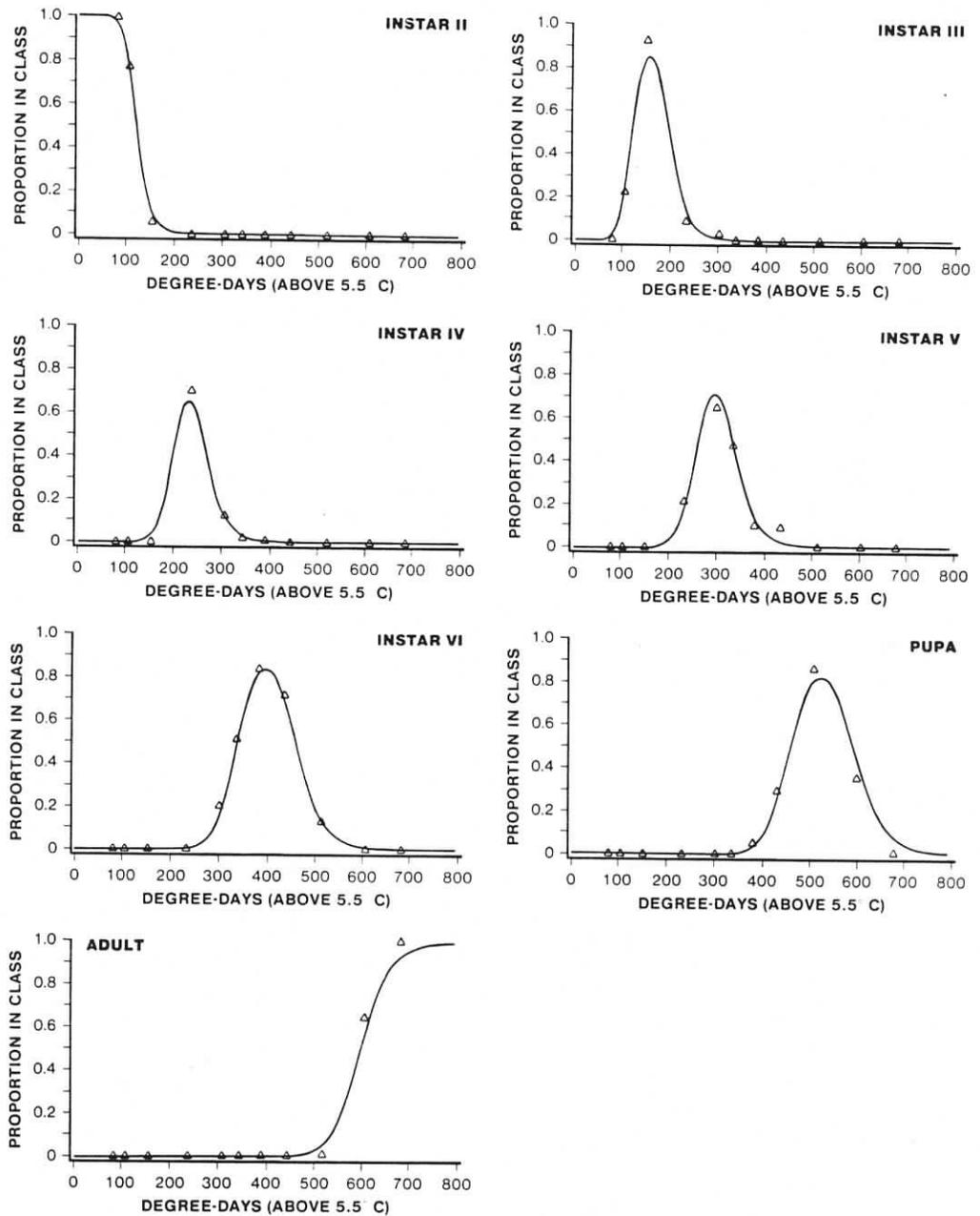


Fig. 1. Comparison of raw data (plotted points) and model results (—) for the proportion of the population (collected on Douglas-fir and grand fir) in each life stage as a function of accumulated DD, Bear Springs plot, Starkey Experimental Forest, Oregon, 1982.

that for instar 6; pupae showed a peak at ca. 540 DD. Model results suggested that adults were present just before 500 DD, and all individuals were adults by 800 DD.

Raw data and phenology model results were compared for western spruce budworms living on grand fir at the Bear Springs plot in 1983 (Fig. 3). In this population, instar 2 was found only before 200 DD. Instars 3 through 5, as estimated by the

model and data, were collected over periods between 200 and 300 DD and had peaks at about 130, 210, and 290 DD, respectively. The sixth instars and pupae again had the greatest ranges (~350-400 DD); peak densities were found at 390 and 520 DD, respectively. As on Douglas-fir (Fig. 2), the first adults were present just before 500 DD, and all were adults at 800 DD (Fig. 3).

Phenology model results were compared with

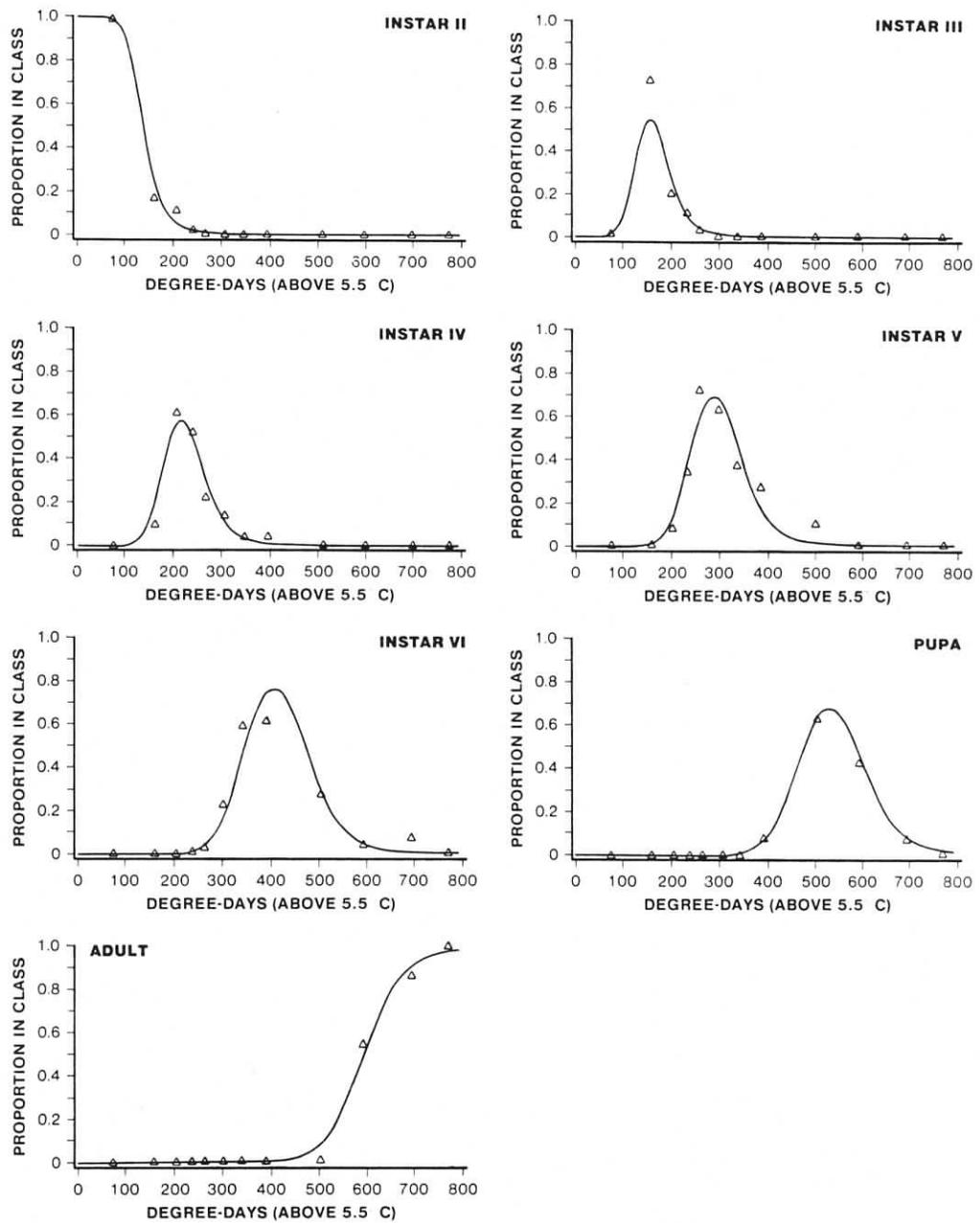


Fig. 2. Comparison of raw data (plotted points) and model results (—) for the proportion of the population (collected on Douglas-fir) in each life stage as a function of accumulated DD, Bear Springs plot, Starkey Experimental Forest, Oregon, 1983.

raw data collected from a population of western spruce budworms living on Douglas-fir on the Meadow Creek plot in 1983 (Fig. 4). Raw data and model results showed that instar 2 was found only before ca. 230 DD. Model results suggest that instars 3 and 4 were found over ranges of 300 and 350 DD, respectively, with peaks at 140 and 230 DD. Instars 5 and 6 were present over similar periods (~350–400 DD) and showed peaks at 320

and 420 DD, respectively. The pupal stage was longest (~500 DD) and showed a peak at 550 DD. Adults were present just before 500 DD, and nearly the entire population was adult by 800 DD.

Raw data and phenology model results were compared for a population of western spruce budworms living on grand fir on the Meadow Creek plot (Fig. 5). Instar 2 was present only before ca. 250 DD. Instars 3 and 4 were present over periods

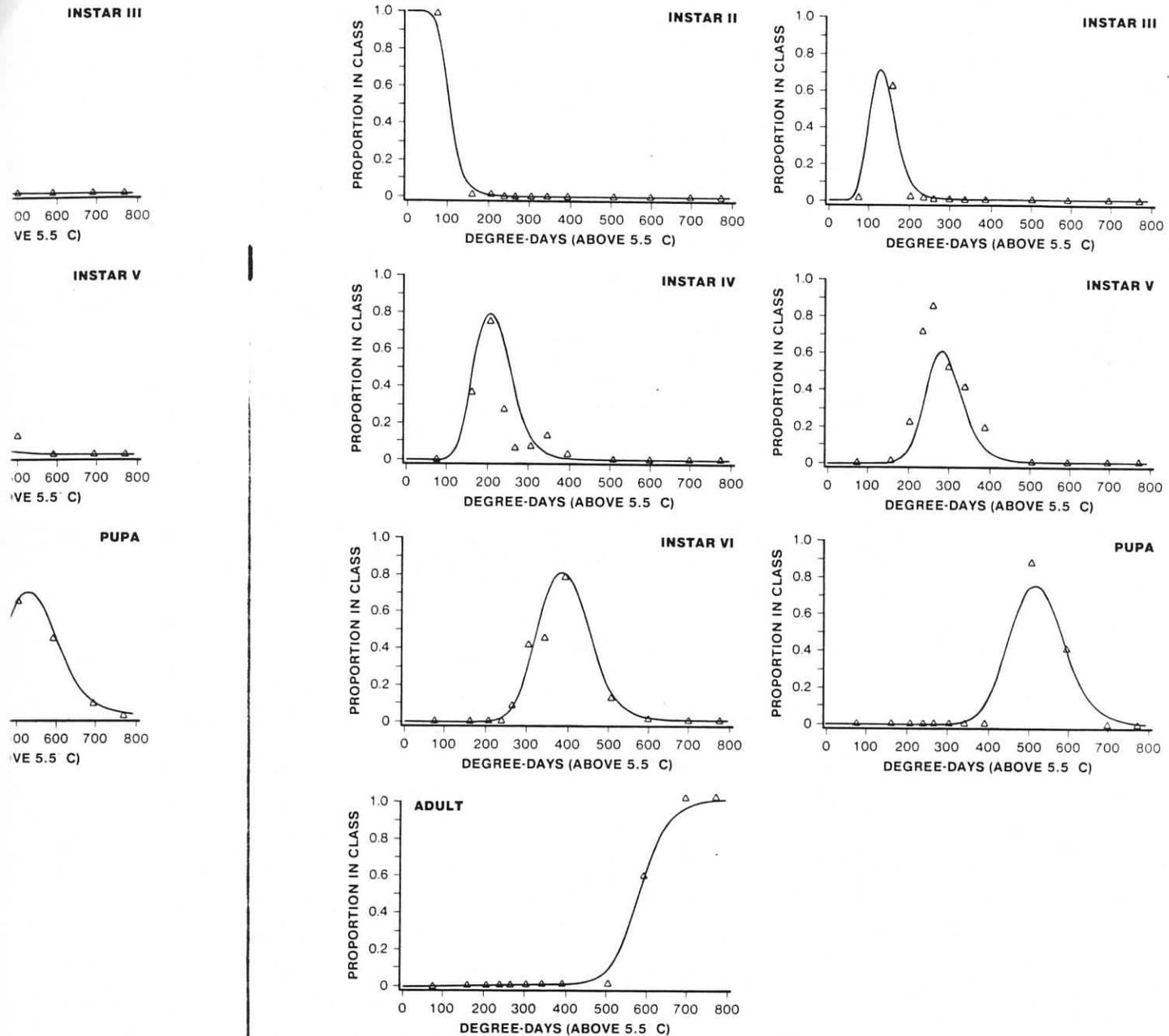


Fig. 3. Comparison of raw data (plotted points) and model results (—) for the proportion of the population (collected on grand fir) in each life stage as a function of accumulated DD, Bear Springs plot, Starkey Experimental Forest, Oregon, 1983.

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The pupal stage was
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present over periods

of 280–300 DD, with peaks at 120 and 210 DD, respectively. Instars 5 and 6 were found over a longer period (~500 DD) than previous stages and showed peaks at 310 and 430 DD. Model results indicated that pupae were present over ca. 500 DD. Adults were present around 450 DD, and nearly all individuals were adults by 800 DD.

Goodness-of-fit tests (Dennis et al. 1986) were not conducted on the data and model results pre-

sented in this study. The χ^2 test was invalid because more than 20% of the cells in the data set had expected frequencies of less than five (Bishop et al. 1975). The model (Dennis et al. 1986) described the development pattern of the western spruce budworm adequately and appears accurate in predicting the modes or the number of DD at which the proportion of the population in a particular developmental stage is greatest (peaks). The

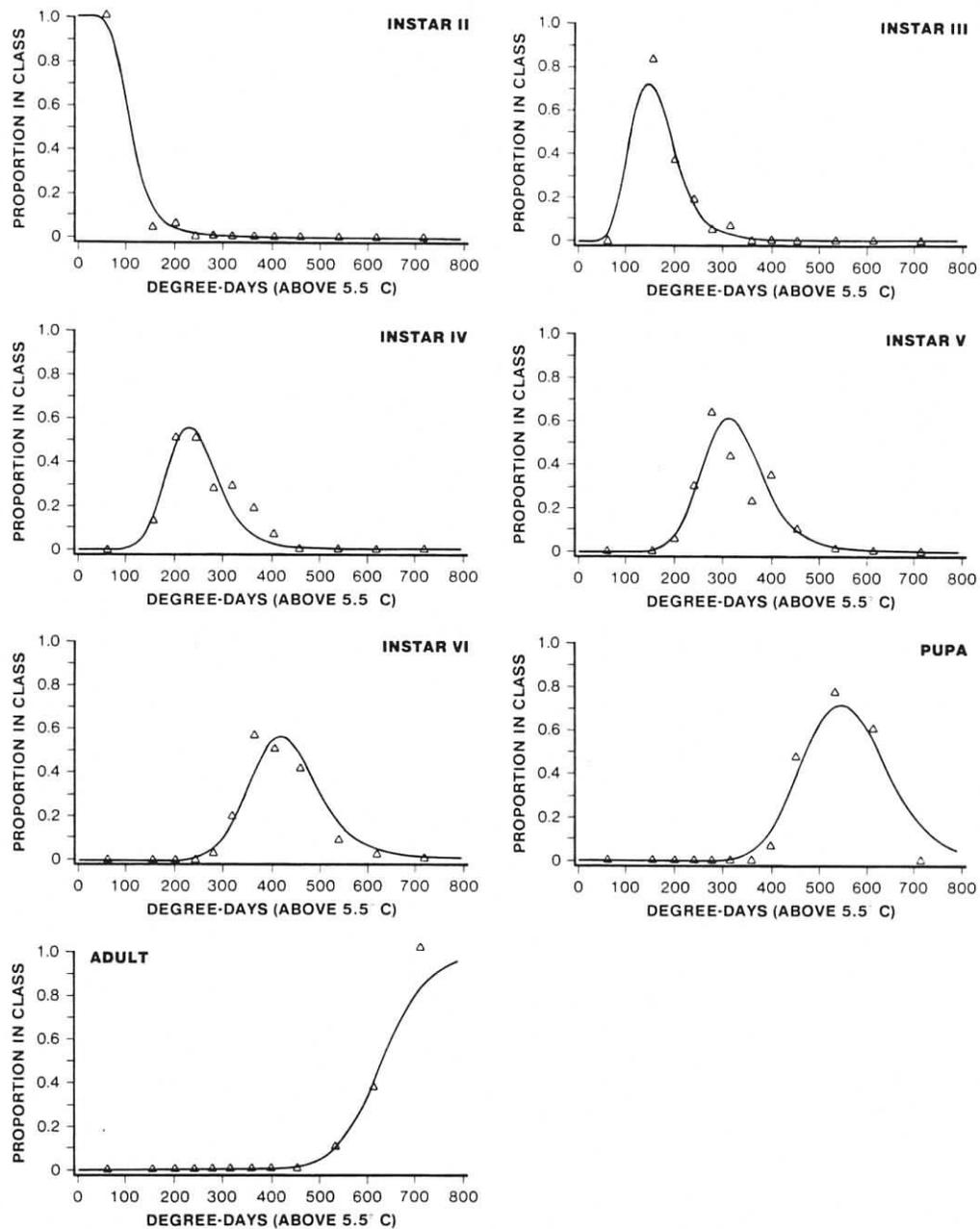


Fig. 4. Comparison of raw data (plotted points) and model results (—) for the proportion of the population (collected on Douglas-fir) in each life stage as a function of accumulated DD, Meadow Creek plot, Starkey Experimental Forest, Oregon, 1983.

counts for occasional cells near the peaks of some developmental stages were underpredicted, however (e.g., Fig. 2, instar 3; Fig. 3, instar 5 and pupa; and Fig. 4, instar 3).

Comparison of Parameters Between Data Sets. Methods described by Dennis et al. (1986) were used to compare all possible pairs of model parameter sets (Table 1). Results always showed significant differences ($\alpha = 0.05$). Minimal overlap of

parameter confidence limits in Table 1 suggested that this was true even before testing. The phenology of western spruce budworms was different in each of the cases we examined.

An individual model parameter worthy of consideration is b^2 , which measures the variability of the data and the resulting individual model. The larger the value of b^2 , the wider the distribution will be at any time (t_i). Biologically, b^2 gives an

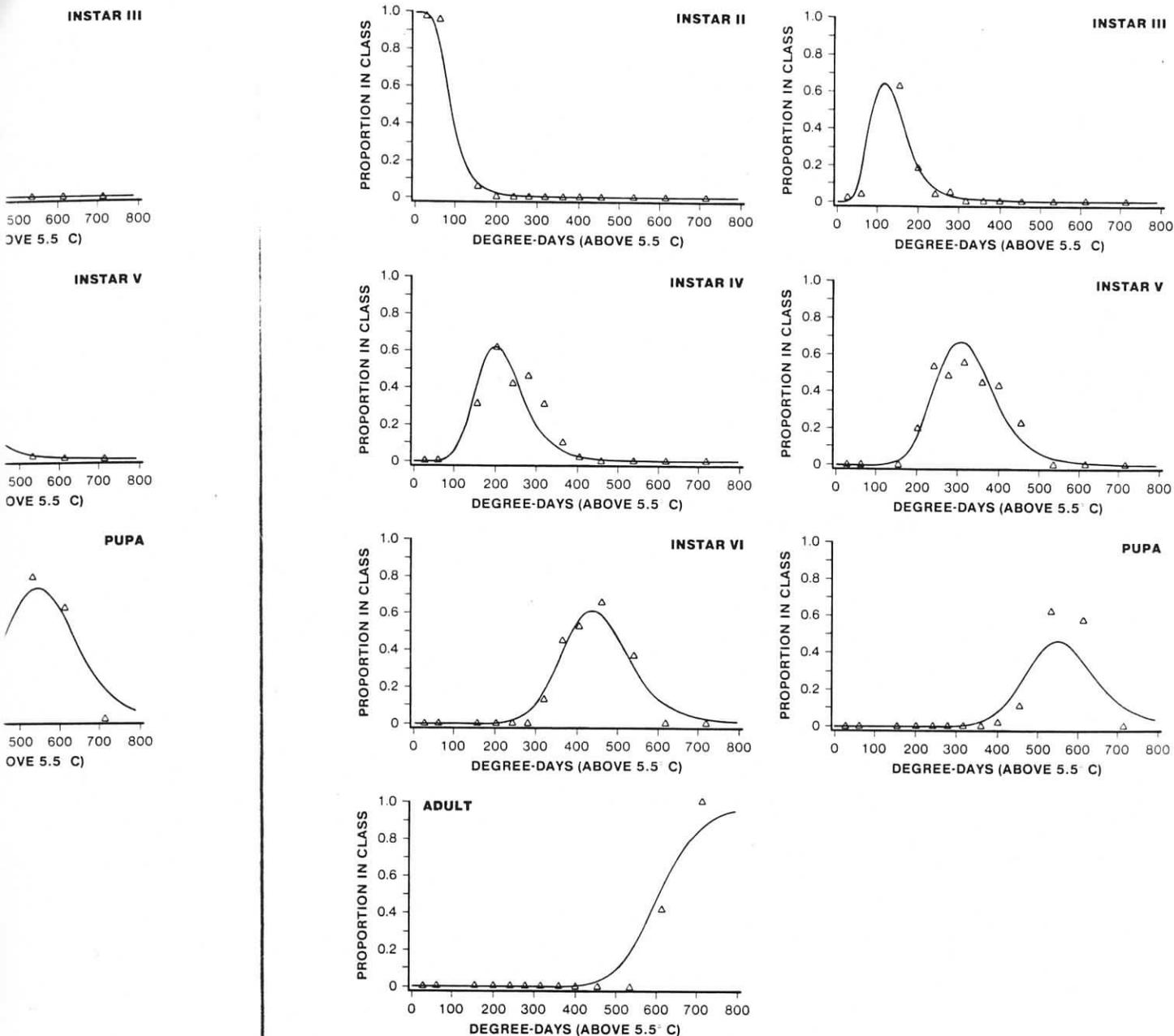


Fig. 5. Comparison of raw data (plotted points) and model results (—) for the proportion of the population (collected on grand fir) in each life stage as a function of accumulated DD, Meadow Creek plot, Starkey Experimental Forest, Oregon, 1983.

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indication of the influence of factors other than DD on western spruce budworm development. If all the variation in development were explained by DD, then b^2 would be 0.

Table 1 shows that the model developed in 1982 for the Bear Springs plot had the smallest b^2 value. Estimated values of b^2 in 1983 were higher in general, but lower on the Bear Springs plot (for both

models) than on the Meadow Creek plot. Defoliation intensities were different between years and plots-within-year. Defoliation of host trees was greater in 1983 than in 1982. In 1983, host trees at Meadow Creek were more severely defoliated than those in 1983 at Bear Springs. These differences in defoliation influenced feeding and development times, and may be partially responsible

for the larger variability and b^2 values in Meadow Creek data sets.

Another factor influencing the b^2 values is the relation between the microclimate, as measured by biophenometer, and the actual microclimate of the western spruce budworm. Foliage characteristics, slope, aspect, elevation, and degree of defoliation of the host species all modify the microclimate of the developing insects. The model formulation that uses DD as a time scale works well (Fig. 1-5). However, differences in b^2 values suggest that additional factors also influenced developmental variability and should be considered for inclusion in future model formulations.

Conclusions. The model form and maximum likelihood procedures accurately describe phenology of the western spruce budworm from instar 2 through adult. This form is an improvement over existing phenology models of western spruce budworm (Wagg 1958); it was more accurate (the likelihood function was greater) and easier to compute than the methods outlined by Osawa et al. (1983), Regniere (1982), and Stinner et al. (1975). Further testing on a variety of phenological data sets will determine whether the model will have widespread utility.

For western spruce budworm, significant differences in the parameter sets of the phenology model (Table 1) by year, plot, and host species suggest the need to improve our understanding of the processes affecting phenology. For formulating integrated pest management strategies, a thorough knowledge of insect and host-plant development both locally and regionally is needed.

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References Cited

- Beckwith, R. C. & W. P. Kemp. 1984. Shoot growth models for Douglas-fir and grand fir. *For. Sci.* 30: 743-746.
- Birley, M. H. 1979. The estimation and simulation of variable development period with application to the mosquito, *Aedes aegypti* (L.). *Res. Popul. Ecol.* 20: 216-226.
- Bishop, Y. M. M., S. E. Fienberg & P. W. Holland. 1975. Discrete multivariate analysis: theory and practice. MIT, Cambridge, Mass.
- Curry, G. L., R. M. Feldman & K. C. Smith. 1978. A stochastic model of a temperature dependent population. *Theor. Popul. Biol.* 13: 197-213.
- Dennis, B., W. P. Kemp & R. C. Beckwith. 1986. Stochastic model of insect phenology: estimation and testing. *Environ. Entomol.* 15: 540-546.
- Kempton, R. A. 1979. Statistical analyses of frequency data obtained from sampling an insect population grouped by stages, pp. 401-418. In J. K. Ord, G. P. Patil & C. Taille [eds.], *Statistical distributions in ecological work*. International Co-operative, Fairland, Md.
- Logan, J. A., R. E. Stinner, R. L. Rabb & J. S. Bache-ler. 1979. A descriptive model for predicting spring emergence of *Heliothis zea* populations in North Carolina. *Environ. Entomol.* 8: 141-146.
- Osawa, A., C. A. Shoemaker & J. R. Stedinger. 1983. A stochastic model of balsam fir bud phenology utilizing maximum likelihood parameter estimation. *For. Sci.* 29: 478-490.
- Read, K. L. O. & J. R. Ashford. 1968. A system of models for the life cycle of a biological organism. *Biometrika* 55: 211-221.
- Regniere, J. 1982. A process oriented model of spruce budworm phenology (Lepidoptera: Tortricidae). *Can. Entomol.* 114: 811-825.
- Regniere, J., R. L. Rabb & R. E. Stinner. 1981. *Popilla japonica*: simulation of temperature development of the immatures, and prediction of adult emergence. *Environ. Entomol.* 10: 290-296.
- Stinner, R. E., G. D. Butler, Jr., J. S. Bache-ler & C. Tuttle. 1975. Simulation of temperature development in population dynamics models. *Can. Entomol.* 107: 1167-1174.
- Wagg, J. W. B. 1958. Environmental factors affecting spruce budworm growth. *Oreg. State Bd. For. Res. Bull.* 11: 1-27.
- Wickman, B. E. 1976. Douglas-fir tussock moth egg hatch and larval development in relation to phenology of grand fir and Douglas-fir in northeastern Oregon. *U.S. For. Serv., Res. Pap. PNW-206*.

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