# A COMPARISON OF TWO TEMPERATURE-DEPENDENT DEVELOPMENT MODELS FOR IMMATURE STAGES OF THE NANTUCKET PINE TIP MOTH (LEPIDOPTERA: TORTRICIDAE)

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#### ABSTRACT

Parameters for a degree-day model (DD) and the Sharpe-DeMichele poikilothermic model (POIK) were estimated for the development of *Rhyacionia frustrana* (Comstock) immature stages. A comparison of the accuracy between the two models was made for eggs, larvae, and pupae. The DD and POIK model were equally effective for predicting development of eggs, but the POIK model was superior for predicting larval and pupal development. Regression analysis of predicted vs. observed development days show a good fit ( $R^2 > 0.99$ ) for eggs using both models, a relative good fit ( $R^2 > 0.90$ ) for larvae and a poor fit ( $R^2 < 0.85$ ) for pupae. Threshold temperatures were at 10.0°C for eggs, 7.0°C for larvae, and 9.8°C for pupae. Optimum hatch was 100% for eggs at 24°C and required 81 DD; optimum survival was 77% for larvae at 21°C and required 704 DD; and optimum eclosion from pupae was 55% at 26°C and required 227 DD.

Key Words: Degree-day, models, *Rhyacionia frustrana*, Nantucket pine tip moth, temperature-dependent, biophysical.

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### INTRODUCTION

Following overwintering, pupal diapause of the Nantucket pine tip moth (NPTM), *Rhyacionia frustrana* (Comstock), accuracy in the prediction of moth flight (Richmond et al. 1983; Malinoski and Paine 1988) and the development of eggs (Berisford et al. 1984) requires information on the temperature-dependent development. Haugen and Stephen (1984) constructed developmental rate curves for NPTM eggs and pupae, estimated a curve for larvae, and calculated the mean thermal units (= degree-day) for each stage. Data for degree-day (DD) requirements have been used successfully for prediction of control timing for insecticide sprays against NPTM (Garguillo et al. 1983, 1984; Malinoski and Paine 1988; Kudon et al. 1988). However, models other than the DD model have not been proposed nor tested for developmental rate of NPTM immature stages.

Since there are discussions about the use of DD models to estimate developmental times (Sharpe and DeMichele, 1977; and Wagner et al. 1984), the DD model was compared to the Sharpe and DeMichele biophysical, poikilotherm model (POIK) for NPTM development. Parameters of the POIK model describe the

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nonlinear response in developmental rates at both high and low temperatures, the linear response at intermediate temperatures, and the entire response curve over a full range of temperatures or over a restricted temperature range (Wagner et al. 1984).

The POIK model describes an exponential increase in developmental rates involving a complex series of reactions of numerous enzyme systems in response to temperature (Sharpe and DeMichele 1977). First, these authors assume that: 1) development is regulated by a single control enzyme whose reaction rate determines the developmental rate of the organism; 2) the developmental rate is proportional to the product of the concentration of active enzymes and their rate constant (which in itself is temperature dependent; and 3) the control enzyme can exist in two temperature-dependent inactivation states as well as an active state. Second, they assume that the control enzyme can exist in one of three energy states; one that predominates at low temperatures, one that predominates over the midtemperature range, and one that predominates at high temperatures. Finally, these authors recognize that if more than one enzyme is evolved in developmental rate, the thermodynamic constants would represent regression coefficients rather than thermodynamic coefficients to a particular rate-controlling enzyme at the temperature considered.

Results obtained from the DD model with a temperature threshold of  $9^{\circ}$ C indicated that predicting emergence of the NPTM from pupae is feasible (Gargiullo et al 1983). Variations in the number of days required for moth emergence from diapausing pupae among different constant temperatures makes the DD approach inaccurate for prediction of development under low and high temperature regimes. Furthermore, developmental rate at controlled temperatures has not been described for NPTM egg and larval stages. This paper compares the DD and POIK models for accurately estimating developmental days of NPTM egg. larval and pupal stages across a wide range of constant temperatures.

## METHODS AND MATERIALS

Eggs deposited in glass vials were held in incubators set at temperatures between 3° and 34°C ( $\pm 0.5$ °C). The number of eggs per incubator ranged from 57 to 120, and hatching eggs were recorded daily. Thirty-five larvae were placed singularly in plastic condiment cups containing artificial diet (Richmond and Thomas, 1976); each cup was placed in incubators set between 3° and 34°C ( $\pm 0.5$ °C), and pupation was monitored every 2-4 days. Sixty pupae were placed in pint-sized paper cups with pierced, transparent covers, held in incubators set between 3° and 34°C ( $\pm 0.5$ °C), and adult emergence was recorded 2 to 3 times each week. The photoperiod was maintained at 12:12 L:D cycle in each incubator using fluorescent tubes. The relative humidity ranged from 40% at 34°C to 80% at 3°C with a slight increase of 5-10% during the dark phase.

The threshold temperature of each stage was estimated by a simple linear regression analysis of the data in Table 1. Estimates of DD required for complete development of the egg, larval, and pupal stages were computed by the following formula:

	DD = D (Tc - Tt)
where	D = mean days of development
	Tc = constant temperature
	Tt = threshold temperature for each stage

For estimation of developmental times by the DD model, it is necessary to assume a constant amount of DD above a threshold. The DD constant for each NPTM immature stage was calculated by averaging DD required across temperatures (Table 1). Estimates of the mean developmental rate of NPTM immature stages on the basis of temperature for the nonlinear POIK model were calculated using the formula and computer program provided by Wagner et al. 1984:

rate = 
$$\frac{\text{RTc}}{298.15} \exp \left[ h(\frac{1}{298.15} - \frac{1}{\text{Tc}}) \right].$$

where

R = the universal gas constant (1.987 cal degree<sup>-1</sup> mole<sup>-1</sup>) Tc = constant temperature h = ratio of enthalpy of activation of the reaction that is

catalyzed by a rate controlling enzyme to R.

Table	1.	Percent egg	hatch,	lar	val survival	l, and	$\mathbf{ecl}$	osion	from	pup	ae and	1 8	associated
		degree-days	(DD)	for	Nantucket	pine	tip	moth	held	at	consta	nt	tempera-
		tures.											

	Eggs*		Larvae*		Pupae*			
Temp.	% Hatch (N)	DD	% Survival (N)	DD	% Eclosion (N)	DD		
9°C	0(80)	-	0(35)	-	-	-		
10	-	-	-	-	0(60)	-		
12	56(68)	70	3(35)	360	-	-		
15	72(57)	86	40(35)	473	-	-		
18	82(120)	78	40(35)	529	7(60)	156		
20	-	-	-	-	18(60)	183		
21	100(82)	87	77(35)	704	-	-		
22	-	-	-	-	20(60)	216		
24	100(112)	81	34(35)	588	13(60)	261		
26	-	-	-	-	55(60)	227		
28	-	-	-	-	35(60)	269		
30	-	-	-	-	33(60)	269		
32	76(80)	84	49(35)	793	20(60)	284		
Average DD		81		575		233		

\*Threshold temperatures for DD were 10.0, 7.0, and 9.8°C for eggs, larvae, and pupae, respectively.

For the POIK model,  $\underline{R}$  and  $\underline{h}$  were estimated as 0.1842 and 8771.1 for eggs, 0.02545 and 6266.7 for larvae, and 0.06325 and 4808.4 for pupae, respectively.

Since there are many ways to calculate  $R^2$  values for nonlinear models and since there are also problems in ascribing significance levels to these  $R^{2's}$  for model comparisons (Kvalseth 1985), we have chosen the simple  $R^{2*}$  (calculated from a predicted vs. observed regression) as an index of goodness-of-fit, with no associated significance levels. Total agreement of predicted vs. observed times would result in  $\mathbb{R}^{2^*} = 1$ , intercept = 0, and slope = 1.0. Thus, the closer the intercept is to zero and the slope to 1.0, the better the model fits the data. In addition, we calculated a weighted least squares index (WLSI) for each model, where WLSI =  $\Sigma$  [(predicted-observed)<sup>2</sup>/predicted]. The lower the WLSI index, the better the model fits.

## **RESULTS AND DISCUSSION**

Percentages of egg hatch, larval survival, and eclosion from pupae at constant temperatures and associated DD for each stage are presented in Table 1. Based upon the highest percent survival and relative lower amount of DD, the optimum developmental temperature was 24°C for eggs, 21°C for larvae, and 26°C for pupae. No survival occurred below 12°C for any stage and survival was reduced below 10% at 12°C for larvae and at 18°C for pupae. Although evidence of embryonic development of eggs and pupae was observed at the lower temperatures, both stages died before completing development. At 34°C, embryonic development was not observed for eggs and pupae, and larvae did not survive. Egg hatch exceeded 50% at temperatures between 12° - 30°C, and hatch was much higher than the 19-44% at  $24\pm2^{\circ}$ C previously reported (Richmond and Thomas, 1976). Survival of larvae and eclosion from pupae were less than 50% at each temperature, except at 21°C for larvae and 26°C for pupae. For eggs, the range of consistency in estimated DD among temperatures was also higher than for either larvae or pupae. The range of DD across all temperatures was 17 for eggs with an average of 81 DD, 433 for larvae with average of 575 DD, and 130 for pupae with an average of 233 DD.

Comparison of the DD and POIK models for predicting developmental days of NPTM immature stages is given in Table 2. The mean developmental days observed for NPTM eggs ranged from  $3.8 \pm 0.1$  days at  $32^{\circ}$ C to  $34.8 \pm 0.3$  days at  $12^{\circ}$ C and was about the same for the number of observed days and for the number of days predicted by the DD and POIK models across all constant temperatures tested. Differences in the number of days for egg development were relatively small, (< 2 d.) between  $15^{\circ}$  and  $32^{\circ}$ C for the observed and predicted values. For eggs, both models fit the observed data (R<sup>2</sup> > 0.99, WLSI < 1.30) (Table 2).

Predicted developmental days for both larvae and pupae by the DD model were substantially different from the observed developmental days, while the predicted developmental days for the two stages by the POIK model were quite similar to those from the observed days. The goodness-of-fit indices indicated that the POIK model provided a considerably more accurate prediction of developmental days for larvae ( $R^2 = 0.92$ , WLSI = 2.2) and pupae ( $R^2 = 0.84$ , WLSI = 0.45) than the DD model did for larvae ( $R^2 = 0.90$ , WLSI = 24.1) and pupae ( $R^2 = 0.74$ , WLSI = 5.6).

The development rate of the egg, larval, and pupal stages of the NPTM are shown in Figure 1. The average observed development rate of eggs and the rates predicted by the DD and POIK models were similar at all temperatures.

The average observed development rate of larvae steadily decreased through 24°C, except at 21°C where the rate showed a substantial increase. Overall the POIK model predicted the development rate of larvae better than the DD model at all temperatures, except at 26°C where the DD model was superior. At the two

Table 2. Comparison of the degree-day (DD) and poikilotherm (POIK) models for predicting developmental days of the egg, larval and pupal stages of the Nantucket pine tip moth.

	Egg deve	elopmer	nt (d.)	Larva de	velopmer	nt (d.)	Pupa d	Pupa development (d.)				
Temp.	Observed Predicted		dicted	Observed	Pre	dicted	Observed	Р	Predicted			
	$(\bar{x}\pm SE)$ *	$DD_{10} = 81$	POIK	(x±SE)	*DD7 =575	POIK	$(\bar{\mathbf{x}}\pm\mathbf{SE})$	*DD <sub>9.8</sub> =233	POIK			
12° C 15 18 20 21 22 24 26 28 30	$34.8\pm0.3$ $17.2\pm0.1$ $9.7\pm0.1$ - $7.9\pm0.1$ - $5.8\pm0.1$ -	40.5 16.2 10.1 - 7.4 - 5.8 - -	35.2 16.7 10.2 - 7.5 - 6.0 - -	$72.0 \pm 0.0 \\ 59.1 \pm 2.9 \\ 48.1 \pm 3.8 \\ 50.3 \pm 3.3 \\ 34.0 \pm 1.5 \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ $	115.0 71.9 52.3 - 41.1 - 33.8 - - -	66.5 58.6 51.8 - 45.9 - 40.9 -	$ \begin{array}{c}     - \\     19.0 \pm 0.0 \\     17.9 \pm 0.5 \\     - \\     17.7 \pm 0.1 \\     18.4 \pm 0.1 \\     14.0 \pm 0.5 \\     14.8 \pm 0.5 \\     13.3 \pm 0.7 \\ \end{array} $	28.4 22.8 - 19.1 16.4 14.4 12.8 11.5	19.7 18.5 - 17.3 16.3 15.3 14.4 13.6			
32	$3.8 \pm 0.1$	3.7	3.8	$31.7 \pm 0.9$	23.0	30.1	$12.8 \pm 0.3$	10.5	12.8			
+R <sup>2</sup> * Intercep Slope WLSI	t	0.991 -1.654 1.182 1.28	0.999 -0.076 1.008 0.070		0.904 -47.286 2.099 24.10	0.918 8.450 0.822 2.20		$0.741 \\ -16.716 \\ 2.108 \\ 5.61$	0.836 1.956 0.878 0.45			

\* This is the average amount of degree-days accumulated at the indicated threshold temperature across all temperatures tested for each stage.

 $+R^2$  is for regression of predicted vs. observed.

lower temperatures, the DD model significantly underestimated the development rate of larvae; and at the highest temperature tested, the DD model significantly overestimated larval development rate.

The range of the average observed development rate of pupae was relatively small, between 0.04 - 0.08, over the range of temperatures tested. The observed rate and the rates predicted by both models were about the same at 22, 24, and 26°C. The predicted development rate of pupae was underestimated at 18 and 20°C, and overestimated at 28, 30, and 32°C by the DD model. The rate predicted by the POIK model at these temperatures was the same as the observed development rate of pupae.

The DD model is now operational and acceptable for predicting the time of spray schedules to control NPTM (Gargiullo et al. 1983, 1984; Malinoski and Paine 1988). Unlike the DD model, the POIK model has not been tested and validated under fluctuating field conditions for NPTM. Salom et al. (1987) reported that parameters determined for the biophysical model (POIK) could be used for actual prediction of egg and larval stage development of the pales weevil, *Hylobius pales* (Herbst). Neither model has been evaluated for all immature stages of the NPTM. Because of the biophysical aspects of the POIK model, however, it can be expected to be more accurate than the DD model. The availability of computers at most research and many field locations makes both laboratory and field evaluation of the POIK model for the NPTM feasible.





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#### LITERATURE CITED

- Berisford, C. W., P. M. Gargiullo, and C. C. Canalos. 1984. Optimum timing for insecticidal control of the Nantucket pine tip moth, Lepidoptera: Tortricidae. J. Econ. Entomol. 77: 174-77.
- Gargiullo, P. M., C. W. Berisford, C. G. Canalos, and J. A. Richmond. 1983. How to time dimethoate sprays against the NPTM. Ga. For. Res. Pap. 44, 11 pp.
- Gargiullo, P. M., C. W. Berisford, C. G. Canalos, J. A. Richmond, and S. C. Cade. 1984. Mathematical descriptions of *Rhyacionia frustrana* (Lepidoptera: Tortricidae) cumulative pheromone trap catch and egg hatch and their use in timing chemical control. Environ. Entomol. 13: 1681-85.
- Haugen, D. A., and F. M. Stephen. 1984. Development rates of Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock) (Lepidoptera: Tortricidae), life stages in relation to temperature. Environ. Entomol. 13: 56-60.
- Kudon, L. H., C. W. Berisford, and M. J. Dalusky. 1988. Refinement of a spray timing technique for the Nantucket pine tip moth (Lepidoptera: Tortricidae). J. Entomol. Sci. 23: 180-86.
- Kvalseth, T. O. 1985. Cautionary note about R<sup>2</sup>. Amer. Stat. 39: 279-85.
- Malinoski, M. K. and T. D. Paine. 1988. A degree-day model to predict Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock) (Lepidoptera: Tortricidae), Flights in southern California. Environ. Entomol. 17: 75-9.
- Richmond, J. A., and H. A. Thomas. 1976. Development of the Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock), under varied photoperiod and crowding conditions on artifical diet. J. Ga. Entomol. Soc. 11: 95-101.
- Richmond, J. A., H. A. Thomas, and H. Bhattacharyya. 1983. Predicting spring flight of NPTM (Lepidoptera: Olethreutidae) by heat unit accumulation. J. Econ. Entomol. 76: 269-71.
- Salom, S. M., F. M. Stephen, and L. C. Thompson. 1987. Development rates and a temperature-dependent model of pales weevil, *Hylobius pales* (Herbst), development. Environ. Entomol. 16: 956-62.
- Sharpe, P. J. H., and D. W. DeMichele. 1977. Reaction kinetics of poikilotherm development. J. Theor. Biol. 64: 649-70.
- Wagner, T. L., H.-I. Wu, P. J. H. Sharpe, R. M. Schoolfield, and R. N. Coulson. 1984. Modeling insect development rates: A literature review and application of a biophysical model. Ann. Entomol. Soc. Am. 77: 208-25.