THE EFFECT OF TEMPERATURE ON THE DEVELOPMENT, GROWTH AND SURVIVAL OF *PSOROPHORA COLUMBIAE*[1]

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ABSTRACT. The effect of temperature on the development rate, growth and survival of an East Texas population of *Psorophora columbiae* was studied by rearing immature mosquitoes at ten constant temperatures: 16, 19, 22, 26, 29, 32, 34, 35, 36 and 39°C. The relationship between development and temperature was described using a recently developed model based on chemical kinetics.

Development rates increased with increasing temperature up to a peak at 34°C. At this temperature, development from eclosion to 50% adult emergence required only 4.5 days. Increases in temperature above 34°C resulted in a decrease in the development rate. The development rate model predicted the observed development rates not only along the linear region at mid-range temperatures, but also along the nonlinear region at high temperatures with a high degree of accuracy ($r^2 = 0.99$).

A significant increase in size, as indicated by head capsule width measurements, was seen with decreasing temperature. This trend was most evident in the 4th larval instar where mean widths ranged from 1.192 mm at 36°C to 1.382 mm at 19°C.

Survival from eclosion to emergence was highest in the range from 26°C (87%) to 34°C (93%). Above and below this range, survival dropped dramatically to 1% at 39°C and 34% at 16°C.

INTRODUCTION

The impact of temperature on insects was emphasized by Andrewartha (1971) who stated, "Temperature influences the speed of development, the duration of life, the fecundity, and the behavior of animals, especially poikilotherms." Information on the impact of temperature on mosquitoes is available for many species (Huffaker 1944, Bar-Zeev 1958, Brust 1967, Parker 1979), and the influence of temperature is an important consideration in the design of mosquito-population and control-strategy models (Haile and Weidhaas 1977, Greever and Georghiou 1979).

The study described herein provides some basic data on the effect of temperature on the development rate, growth and survival of immature stages of an East Texas population of *Psorophora columbiae* (Dyar and Knab). The development rate curve is described using the model of Sharpe and DeMichele (1977). This information will serve as the basis for the future development of population models of *Ps. columbiae* which can be used by mosquito control practitioners to better forecast the dynamics of this species in Texas riceland ecosystems.

MATERIALS AND METHODS

GENERAL. Mosquito eggs used in these studies were obtained from wild-caught *Ps. columbiae* females collected at Anahuac, Chambers County, TX on 27 May and 5 June 1980. The eggs were stored at 26°C and 90–100% RH until they were hatched.

Eggs were hatched at room temperature using the hatching tube method of Novak and Shroyer (1978) and a solution of 0.55 mg Bacto dehydrate nutrient broth (Difco Laboratories, Detroit, MI) in 225 ml deionized water. Only the larvae hatching during the first 2 hr were used, and the development time was assumed

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to have begun at the mid-point of the 2 hr period. Twenty-five larvae were put in each of 4 enameled pans (18 × 30 cm) filled with ca. 800 ml of deionized water stabilized at the desired temperature.

The 4 enameled pans were floated in a large water bath incubator. The temperature of the bath was controlled with an immersible thermometer (Philadelphia Thermometer Co., Phil., PA) and a switching device and heat lamp arrangement described by Anderson (1963)[3]. The temperature in the pans was monitored with a Rustrak® 2144 temperature probe (Gulton Ind. Inc., Manchester, NH). There was no discernible variation in the water temperature during the experiments. A daily light:dark cycle of 14:10 was used during all experiments. The use of the heat lamps, however, intermittently exposed the larvae to dim, indirect light. It was assumed that this exposure did not significantly affect development rates.

Because of cooling limitations in the room in which the water baths were kept, rearing experiments at 19°C and below were conducted in an environmental cabinet. All other procedures were similar to those used with the water bath.

Larvae were fed a 1:1:1 (by weight) mixture of brewer's yeast, lactalbumin and ground rodent lab chow. Seven ml of deionized water and 170 mg of the diet were mixed into a slurry and the larvae were fed 0.5 ml of the slurry per pan per day. On the day during which the larvae reached the third instar, they were given an additional 0.5 ml (1.0 ml total) of the diet slurry.

The larvae were examined 4 times daily and the larval exuviae were collected, determined as to instar and counted. Upon pupation, the pupae were transferred to a glass chimney emergence cage (Cocke 1976)[4] and held in the environment cabinet at the appropriate temperature (±0.5°). The pupae were also checked 4 times daily, and the emerged adults were sexed and counted. Voucher specimens of the larval and pupal exuviae were mounted on glass slides. This procedure was repeated at 16, 19, 22, 26, 29, 32, 34, 35, 36 and 39°C.

DEVELOPMENT RATE. All molts were assumed to have occurred at the midpoint of the check interval. The median molt was selected as the dividing point between instars, and was used to determine the time required to complete any stage of development. For each temperature, all molts into a given instar were plotted as a cumulative frequency vs. time post-eclosion; and the median molt was estimated graphically.

MODEL. The development rate data were described using the model developed by Sharpe and DeMichele (1977). For simplicity, the model assumes that development rate, although a product of a complex series of genetic and biochemical events, is under the control of a single enzyme. This enzyme may exist in an active state or be reversibly inactivated at high or low temperatures. The model was modified algebraically by Schoolfield et al. (1981) to facilitate parameter estimation and to reduce high correlations between parameter estimators, thereby facilitating nonlinear regression. The data indicated use of a 4-parameter version of the Schoolfield model to reflect only high temperature inhibition. This version of the model has the form:

$$r(T) = \frac{\rho(25°C)\,\frac{T}{298}\exp\left(\frac{\Delta H_A^{\ddagger}}{R}\left(\frac{1}{298} - \frac{1}{T}\right)\right)}{1 + \exp\left(\frac{\Delta_H}{R}\left(\frac{1}{T_{1/2_H}} - \frac{1}{T}\right)\right)} \quad (1)$$

[3] Anderson, D. F. 1963. Effect of thermal stress on dimorphism of subarctic aedine mosquitoes (Diptera: Culicidae). Unpublished Ph.D. Thesis, Univ. Illinois, Urbana. 97 pp.

[4] Cocke, J. 1976. Fluorescent insect growth regulators (FIGR): Their effects on *Aedes aegypti* (L.) (Diptera: Culicidae), and potential use in studying insect hormone and growth regulator action. Unpublished Ph.D. Dissertation, Texas A&M Univ., College Station. 136 pp.

where;
r(T) is the development rate at temperature T(time^{-1}),
T is temperature in Kelvin degrees (298°K = 25°C),
R is the universal gas constant (1.987 cal deg^{-1} mole^{-1}),
ρ(25°C) is the development rate at 25°C assuming no enzyme inactivation (time^{-1}),
$\Delta H_A^{\neq}$ is the enthalpy of activation of the reaction that is catalyzed by the enzyme (cal mole^{-1}),
$T_{½H}$ is the temperature (°K) at which the enzyme is ½ active and ½ high temperature inactive.
ΔH_H is the change in enthalpy associated with high temperature inactivation of the enzyme (cal mole^{-1}).

An Arrhenius plot (log of development rate vs. reciprocal of absolute temperature) was used to graphically determine initial parameter estimates for ρ(25°C) (0.006hr−1) and $T_{½H}$ (313°K). Initial estimates for $\Delta H_A^{\neq}$ and ΔH_H were arbitrarily set at 10,000 cal mole^{-1} and 100,000 cal mole^{-1}, respectively (Schoolfield et al. 1981). A nonlinear regression using the Marquardt estimation technique[5] was performed to determine final estimates of model parameters and to fit the model to the laboratory data.

GROWTH. The head capsule width of shed skins was used as an index of size. About 25 head capsules were measured for each instar at each temperature. The head capsules were immersed in alcohol in a glass depression slide and were measured at their widest point under a binocular microscope. A Duncan's multiple range test corrected for unequal sample sizes (Kramer 1956) was performed to test for significant differences in widths for mosquitoes reared at different temperatures (Steel and Torrie 1980).

SURVIVAL. Survival was calculated as the percent of those larvae beginning an experiment which successfully emerged as adults. A Duncan's multiple range test with an arc sine transformation, using each pan of larvae as a replicate, was used to test for significant differences in survival between temperatures (Steel and Torrie 1980).

RESULTS AND DISCUSSION

DEVELOPMENT RATE. The times required for completion of each instar at each temperature are summarized in Table 1. Total hours represent the total time for development from eclosion to 50% adult emergence. The development rate, or inverse of the total hours, is also shown in Table 1. The trend in these rates is similar to that reported for *Psorophora confinnis* (Lynch-Arribálzaga) (Gunstream and Chew 1967). The 26°C development rate in the present study is in close agreement with the 79°F data presented by Horsfall (1942) for an Arkansas population of *Ps. columbiae*. The development rates were lowest at low temperatures and increased with increasing temperature. The development rates for *Ps. columbiae* reached a peak at 34°C and then declined with further increases in temperature. Chastant (unpublished data) determined that water temperatures likely to be encountered by larval mosquitoes along the Texas Coast range from about 20° to 37°C. A maximum development rate at 34°C in the lab suggests that the immature stages of this mosquito are well adapted to the temperatures they might reasonably expect to encounter, and that only at high temperature extremes might they be adversely affected.

MODEL. Table 2 and Fig. 1 compare laboratory development rate data with model predicted rates. These data demonstrate that the model can describe the development rate data for this mosquito population reared at constant temperatures with extreme accuracy (r^2 = 0.99). While more complex than other development rate models, this model has certain advantages which recommend its use. Particularly noteworthy is the model's ability to correctly predict development rate values in the area of nonlinearity at high temperatures. This is the region in which most empirical, day-degree models de-

[5] Statistical Analysis System (SAS 79.5), SAS Institute Inc., Cary, NC.

part from observed data. Additionally, this model attempts to describe the underlying mechanisms involved in development, not just the resulting development rate curve. This realistic approach to modeling increases awareness and understanding of the system under study whereas empirical modeling does not.

The data could form the basis of a larger simulation model for *Ps. columbiae* populations. With additional information on egg longevity and diapause, adult life-table characteristics, and fecundity, the model could provide insight to the effectiveness of various control strategies.

GROWTH. In general, size decreases as temperature increases. In the case of our study, ranges of head capsule mean width for the larval instars in mm were: L_1, 0.325–0.425; L_2, 0.50–0.70; L_3, 0.80–1.075 and L_4, 1.10–1.50. The relationship between size and temperature was most evident in the fourth instar for the *Ps. columbiae* populations used in the present

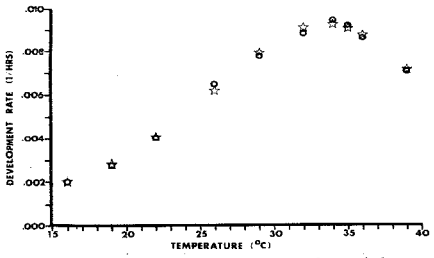

Fig. 1. Plot of observed (0) and model predicted(*) development rates vs. Celsius temperature for *Psorophora columbiae* reared at various constant temperatures.

Table 1. Hours in stage and development rates for *Psorophora columbiae* reared at various constant temperatures.

Temperature (°C)	Hours in larval instar I	II	III	IV	Hours in pupal stage	Total hours	Development rate (1/total hrs)
16	108	81	107	142	52	491	0.0020
19	66	55	61	99	81	362	0.0028
22	69	30	39	58	52	248	0.0040
26	27	24	24	42	32	153	0.0065
29	24	20	19	39	26	128	0.0078
32	22	13	17	38	22	112	0.0089
34	18	14	15	36	22	105	0.0095
35	24	14	13	36	21	108	0.0092
36	23	15	16	39	22	115	0.0087
39	—	—	—	—	—	141	0.0071

Table 2. Summary data for observed and model predicted* rates for the development of *Psorophora columbiae* reared at various constant temperatures.

Temperature (°C)	Observed time (hr)	Model time (hr)	Observed rate (1/hr)	Model rate (1/hr)	Rate Error
16	491.00	498.6	0.0020	0.0020	0.000028
19	362.00	346.3	0.0028	0.0029	−0.000129
22	248.00	244.5	0.0040	0.0041	−0.000060
26	153.00	160.9	0.0065	0.0062	0.000321
29	128.00	125.8	0.0078	0.0080	−0.000139
32	112.00	109.0	0.0089	0.0092	−0.000246
34	105.00	107.3	0.0095	0.0093	0.000207
35	108.00	109.5	0.0092	0.0091	0.000123
36	115.00	113.7	0.0087	0.0088	−0.000102
39	141.00	140.4	0.0071	0.0071	−0.000029

* Final parameter estimates: $\rho(25°C)$, 0.0059; ΔH_A, 20183.4; ΔH_H, 51213.9, $T_{1/2H}$, 308.0

Table 3. Summary statistics and results of Duncan's multiple range test (corrected for unequal sample sizes) for 4th instar head capsules width measurements of *Psorophora columbiae* reared at various constant temperatures.

Temperature (°C)	N./	Mean (mm)	S.D.	Significance*
19	18	1.38	0.06	A
22	35	1.37	0.06	A B
16	32	1.35	0.04	B
26	25	1.32	0.07	C
29	29	1.30	0.03	C
34	25	1.26	0.05	D
35	23	1.25	0.04	D
32	25	1.25	0.05	D
39	1	1.30	—	E D
36	36	1.19	0.05	E

* Means with the same letter are not significantly different ($P<0.05$).

Table 4. Summary statistics and results of Duncan's multiple range test for survival from eclosion through adult emergence of *Psorophora columbiae* reared at various constant temperatures.

Temperature (°C)	N./*	Mean survival (%)	S.D.	Significance**
34	4	93.0	5.0	A
32	4	88.0	12.6	A
26	4	87.0	3.8	A
29	4	83.0	12.7	A
19	4	50.0	19.1	B
22	4	37.0	14.0	B
35	4	35.0	3.8	B
16	4	34.0	26.6	B
36	4	32.0	16.9	B
39	4	1.0	2.0	C

* Number of pans each initially containing 25 larvae.

** Means with the same letter are not significantly different ($P<0.05$).

study (Table 3). This is not surprising since, by the molt to the pupal stage, the mosquitoes have been under the influence of a given temperature for the previous 4 larval instars. Since the 4th instar is also the last immature stage which feeds, the sizes of the 4th instar head capsules provide a good indicator of the relative sizes of the resulting adults.

The reasons for the inverse relationship between temperature and growth are not clear, but Laudien (1973) suggested that it may be the result of rapid development at higher temperatures. Although the growth rate may increase with temperature, this increase is outweighed by a decrease in the time available for growth, and the resulting insect is smaller.

SURVIVAL. Survival data and results of the Duncan's test are summarized in Table 4. These data show a region of high survival at mid-range temperatures, with survival dropping off above and below this region.

This suggests that temperatures in a range normally encountered by the immatures in a field situation are not in themselves deleterious. Survival in the field, however, may also be indirectly affected by temperature. An increase in the length of the immature stages at lower temperatures may increase their exposure to pathogens, predators or parasites. Conversely, high temperatures may encourage the growth of harmful bacteria or other organisms detrimental to survival.

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