Temperature-Dependent Development and Survival Rates of *Culex quinquefasciatus* and *Aedes aegypti* (Diptera: Culicidae)

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ABSTRACT   Development, growth, and survival of *Culex quinquefasciatus* Say and *Aedes aegypti* (L.) were determined at six constant temperatures (15, 20, 25, 27, 30, 34°C). The Sharpe & DeMichele four-parameter model with high-temperature inhibition described the temperature-dependent median developmental rates of both mosquito species. In both species, body size generally decreased as temperature increased. Head capsule widths in all instars in both species were significantly greater at 15 than at 30–34°C. Except for the third instar of *Ae. aegypti*, the larval body lengths in both species were significantly greater at 15 than at 34°C. All instars and pupae of both species and the adults in *Cx. quinquefasciatus* were significantly heavier at 15 than at 27–34°C. In *Cx. quinquefasciatus*, survival from eclosion to adult emergence was highest in the range from 20 to 30°C (85–90%) and dropped drastically at 15 (38%) and 34°C (42%). In *Ae. aegypti*, survival to adult stage was high at 20 (92%) and 27°C (90%) and lowest at 15°C (3%).

KEY WORDS   Insecta, temperature-dependent development, *Culex quinquefasciatus*, *Aedes aegypti*

INFORMATION ON THE EFFECTS of temperature on the rates of development and survival of the various stages of mosquitoes are necessary in designing population and control strategy models (Wagner et al. 1975, Moon 1976, Haile & Weidhaas 1977, Greever & Georghiou 1979). Data on the effects of temperature on the development of *Culex quinquefasciatus* Say (Shelton 1973, Madder et al. 1983, Rayah & Groun 1983, Kasule 1986, Service 1986) and *Aedes aegypti* (L.) (Bar-Zeev 1958, Kasule 1986, Southwood et al. 1972) have been reported. Unfortunately, the reported data were not collected in the appropriate form or published in sufficient detail to provide the distributions of values required for calculations in mathematical models of temperature-dependent development. Because of variation among individuals, populations must be sampled at several time intervals to document the distribution of development times. Closer sampling intervals are required at high temperatures than at low temperatures to obtain approximately equal numbers of data points within the range of the distribution.

In the study reported here, the effect of constant temperatures on the developmental rates, growth, and survival of the immature stages of *Cx. quinquefasciatus* and *Ae. aegypti* was determined under laboratory conditions, and the temperature-dependent model of Sharpe & DeMichele (1977) was used to describe developmental rates. The distribution of development was described using the approach of Stinner et al. (1975).

Materials and Methods

Mosquito eggs used in these studies were obtained from laboratory colonies whose stock parents originated from Raleigh, N.C., within the previous 2 yr. Larvae hatching during the first hour after the eggs were placed on water at 27°C were used, and the developmental time was assumed to be at the midpoint of this 1-h period. One larva was placed in each well (7 ml) of a covered 12-well tissue culture plate (Cat. 25815; Corning Company, Corning, N.Y.) containing 3 ml liver solution (0.26 mg liver powder/ml deionized water). Thirty plates were placed in each of five incubators (maintained at 15, 20, 25, 30, and 34°C) and in a controlled-environment room (27°C). Every second day, first and second instars were provided with 30 μl of liver solution per well, and third and fourth instars were given 50 μl. Water was added as needed to maintain the volume. Based on our observations of liver particles being present at all times in the cells, this feeding regimen provided excess food for the larvae at all temperatures. The incubators and the controlled room were illuminated continuously with fluorescent light. In a preliminary experiment, this procedure for rearing individual larvae in tissue culture plates under constant light was compared with our routine rearing in groups in pans under a 14:10 (L:D) photoperiod, and no differences in development times were observed.

Mosquito larvae were examined at intervals of

Table 1. Mean, median, and predicted median number of days for development of *Cx. quinquefasciatus* from egg hatch to adult emergence at six constant temperatures (15–34°C)

Life stage	Temp, °C	n^a	Days to complete each life stage		
			Observed mean ($\pm$SE)^b	Observed median	Predicted median
First instar	15	348	5.79 (0.09)a	5.84	4.47
	20	352	1.85 (0.02)b	1.87	2.17
	25	350	1.39 (0.04)c	1.45	1.26
	27	350	0.97 (0.01)d	0.97	1.09
	30	338	0.99 (0.01)d	0.99	0.94
	34	360	0.84 (0.01)d	0.89	0.90
Second instar	15	279	4.56 (0.13)a	4.47	3.97
	20	330	1.64 (0.02)b	1.64	1.86
	25	317	1.44 (0.02)b	1.42	1.04
	27	328	0.71 (0.01)c	0.69	0.89
	30	314	0.89 (0.01)c	0.88	0.77
	34	354	0.79 (0.01)c	0.73	0.74
Third instar	15	230	6.43 (0.21)a	5.22	3.84
	20	274	1.98 (0.08)b	1.82	2.17
	25	275	1.65 (0.04)b	1.69	1.39
	27	246	1.03 (0.03)c	1.02	1.22
	30	243	1.24 (0.05)c	1.19	1.07
	34	259	1.10 (0.04)c	1.03	1.05
Fourth instar	15	161	8.57 (0.19)a	8.14	6.94
	20	207	4.06 (0.06)b	4.07	4.68
	25	228	3.47 (0.08)c	3.44	3.20
	27	200	2.67 (0.05)d	2.68	2.76
	30	178	2.29 (0.03)d	2.28	2.26
	34	182	2.45 (0.08)d	2.36	2.37
Pupa	15	52	6.03 (0.21)a	5.98	4.71
	20	164	2.54 (0.04)b	2.50	2.98
	25	178	2.33 (0.03)b	2.36	2.03
	27	166	1.65 (0.04)c	1.64	1.82
	30	145	1.79 (0.05)c	1.71	1.65
	34	73	1.84 (0.07)c	1.72	1.72
Total^c	15	52	31.35 (0.46)a	31.10	27.19
	20	164	12.07 (0.14)b	12.09	13.82
	25	178	10.52 (0.12)c	10.50	8.72
	27	166	7.07 (0.05)d	7.02	7.79
	30	145	7.21 (0.06)d	7.07	7.07
	34	73	7.08 (0.06)d	6.97	6.91

^{a} Total completing each life stage.

^{b} Means followed by the same letter within each life stage are not significantly different ($P > 0.05$; Tukey's test [SAS Institute 1982]).

^{c} Egg hatch to adult emergence.

Table 2. Mean, median, and predicted median number of days for development of *Ae. aegypti* from egg hatch to adult emergence at six constant temperatures (15–34°C)

Life stage	Temp, °C	n^a	Days to complete each life stage		
			Observed mean ($\pm$SE)^b	Observed median	Predicted median
First instar	15	318	7.67 (0.14)a	7.68	7.87
	20	337	2.67 (0.11)b	2.55	3.39
	25	284	2.74 (0.12)b	2.69	1.59
	27	344	0.96 (0.03)c	0.98	1.26
	30	284	1.18 (1.07)cd	1.16	1.07
	34	254	1.42 (0.03)d	1.40	1.43
Second instar	15	190	8.88 (0.40)a	8.19	7.02
	20	301	1.43 (0.11)b	1.45	2.37
	25	242	1.35 (0.05)b	1.27	0.96
	27	291	0.77 (0.03)b	0.71	0.78
	30	240	0.89 (0.05)b	0.86	0.82
	34	211	1.31 (0.04)b	1.31	1.51
Third instar	15	93	14.97 (0.83)a	13.92	10.99
	20	262	1.62 (0.05)b	1.61	3.32
	25	172	1.37 (0.06)b	1.48	1.27
	27	251	0.96 (0.03)b	0.99	0.99
	30	201	0.98 (0.03)b	0.93	0.84
	34	167	0.84 (0.04)b	0.85	0.95
Fourth instar	15	30	15.31 (1.22)a	16.03	14.06
	20	221	3.59 (0.07)b	3.45	5.37
	25	139	3.15 (0.06)bc	3.26	2.51
	27	207	1.78 (0.03)d	1.78	2.03
	30	161	1.94 (0.04)cd	1.91	1.67
	34	130	1.49 (0.05)d	1.48	1.58
Pupa	15	4	8.49 (1.13)a	8.46	6.90
	20	162	3.11 (0.07)b	3.04	4.10
	25	75	3.03 (0.04)b	2.98	2.50
	27	142	1.79 (0.03)c	1.81	2.06
	30	127	1.82 (0.04)c	1.79	1.56
	34	97	1.09 (0.03)d	1.05	1.08
Total^c	15	4	55.33 (3.55)a	58.31	47.85
	20	162	12.43 (0.19)b	12.49	18.61
	25	75	11.72 (0.11)b	11.57	8.86
	27	142	6.36 (0.04)c	6.49	7.30
	30	127	6.86 (0.04)c	6.89	6.32
	34	97	6.15 (0.05)c	6.29	6.67

^{a} Total completing each life stage.

^{b} Means followed by the same letter within each life stage are not significantly different ($P > 0.05$; Tukey's test [SAS Institute 1982]).

^{c} Egg hatch to adult emergence.

4–8 h for molting (determined by the presence of exuviae). Molting was considered to have occurred at the midpoint of the time interval preceding the time when the molt was detected.

Larval wet weights, body lengths, head capsule widths of the exuviae, and the wet weights of pupae and adults were determined by destructive sampling. Twenty specimens of each instar (four specimens in each of five replicates) were used for each species and each temperature for the measurements of larvae, larval exuviae, and pupae. Larval length was measured from the most anterior part of the head to the posterior margin of the 10th abdominal segment under a binocular microscope. The larvae and pupae were sponged free of water with a piece of filter paper before they were weighed. The head capsules of the larval exuviae

were immersed in 70% ethyl alcohol in a glass depression slide and measured at their maximum width under a binocular microscope. Thirty adults (15 males and 15 females at each temperature) were aspirated from the wells, anesthetized with carbon dioxide, and weighed individually within 1 h after emergence. Morphometric data were tested by analysis of variance using a general linear model (GLM) procedure (SAS Institute 1982).

Survival was based on the number of the larvae at the start of each experiment and was calculated for each instar and stage. After arcsine transformation of the data, differences in survival among temperatures were tested for significance using Tukey's test ($P = 0.05$).

For each mosquito species, the four-parameter version of the Sharpe & DeMichele (1977) nonlin-

Table 3. Parameter estimates for the Sharpe & DeMichele model (Equation 1) and R^2 of the model fit to observed median development rates of *Cx. quinquefasciatus* and *Ae. aegypti*

Life stage	RH025	HA	TH	HH	R^2
		Cx. quinquefasciatus			
First instar	1.23439	27,534.92	301.00	37,071.82	0.99
Second instar	1.42950	28,219.93	301.37	39,340.77	0.97
Third instar	0.94308	20,767.22	304.00	36,213.96	0.98
Fourth instar	0.31230	12,629.46	308.31	140,281.42	0.97
Larvae[a]	0.21554	24,689.00	301.82	37,270.21	0.99
Pupa	0.55490	15,648.63	306.60	43,983.41	0.99
Total[b]	0.21945	28,049.98	298.60	35,362.18	0.99
		Ae. aegypti			
First instar	0.68007	28,033.83	304.33	72,404.07	0.95
Second instar	1.24508	36,400.55	301.78	81,383.14	0.96
Third instar	1.06144	41,192.69	301.29	60,832.62	0.97
Fourth instar	0.57065	34,455.89	301.44	45,543.49	0.97
Larvae[a]	0.20429	36,072.78	301.56	59,147.51	0.97
Pupa	0.74423	19,246.42	302.68	5,954.35	0.98
Total[b]	0.15460	33,255.57	301.67	50,543.49	0.98

[a] First through fourth instars.
[b] Egg hatch to adult emergence.

ear model of temperature-dependent poikilotherm processes was used to describe the effect of constant temperature on median development rate (reciprocal of median number of days to complete development). The Sharpe & DeMichele model with high temperature inhibition is shown in Equation 1:

$$r(K) = \frac{\text{RH025}\,\dfrac{K}{298.15}\cdot\exp\left[\dfrac{\text{HA}}{1.987}\left(\dfrac{1}{298.15} - \dfrac{1}{K}\right)\right]}{1 + \exp\left[\dfrac{\text{HH}}{1.987}\left(\dfrac{1}{\text{TH}} - \dfrac{1}{K}\right)\right]} \quad (1)$$

where $r(K)$ is the median development rate (days^{-1}) at temperature K (°Kelvin = °C + 273.15). RH025, HA, TH, and HH are parameters estimated by a nonlinear regression routine outlined by Wagner et al. (1984) for use in the NLIN procedure (SAS Institute 1982). Once the parameters are determined, the equation can be used to calculate development rates at any temperature and used in a population simulation model with variable temperature input. Schoolfield et al. (1981) discuss the biological significance of these parameters.

Model parameters were estimated for each life stage (i.e., first, second, third, fourth instars, pupa), combined development time of first to fourth larval stadia, and total development time from egg hatch to adult emergence. In each case, the goodness of fit was tested using a linear regression of the predicted versus observed values to calculate R^2 and was tested for a slope of 1 and intercept of 0 (REG procedure) (SAS Institute 1982).

Development rates of insects exposed to constant temperature cannot be assumed to be normally distributed. Therefore, the approach of Stinner et al. (1975) was used to construct a model for vari-ation in the total time from egg hatch to adult emergence. For each temperature, median physiological ages at first and last emergence were calculated. These physiological ages were averaged over all temperatures, resulting in a median of 0.89 at first emergence and 1.17 at 100% emergence. By definition, 50% emergence occurs at a median physiological age of 1.0. The cumulative proportion of the mosquito population completing development (y) at median physiological age (p) is described by Equation 2:

$$y = (1 - z)^{2.0126z^2} \quad (2)$$

Here, $z = (1.17 - p)/(1.17 - 0.89)$. Thus, the distribution of development is expressed as a function of the median physiological age, and this relationship remains constant over all temperatures. The median physiological age at any time (days) at any temperature is calculated by multiplying the estimated median rate of development at that temperature by that chronological time (days).

Results and Discussion

The observed development times (mean and median) and the predicted medians calculated from the Sharpe & DeMichele (1977) model (Equation 1 and parameters in Table 3) for *Cx. quinquefasciatus* and *Ae. aegypti* are given in Tables 1 and 2. For *Cx. quinquefasciatus*, there was a significant decrease in the number of days required for total development (from egg hatch to adult emergence) between temperatures of 15–27°C but no further significant decrease at 30 and 34°C. A similar trend of significant decrease in development times was observed for all larval stadia and the pupal stage. For *Ae. aegypti*, a significant decrease in number of days required for development in second and third stadia at 15–20°C was observed. No further
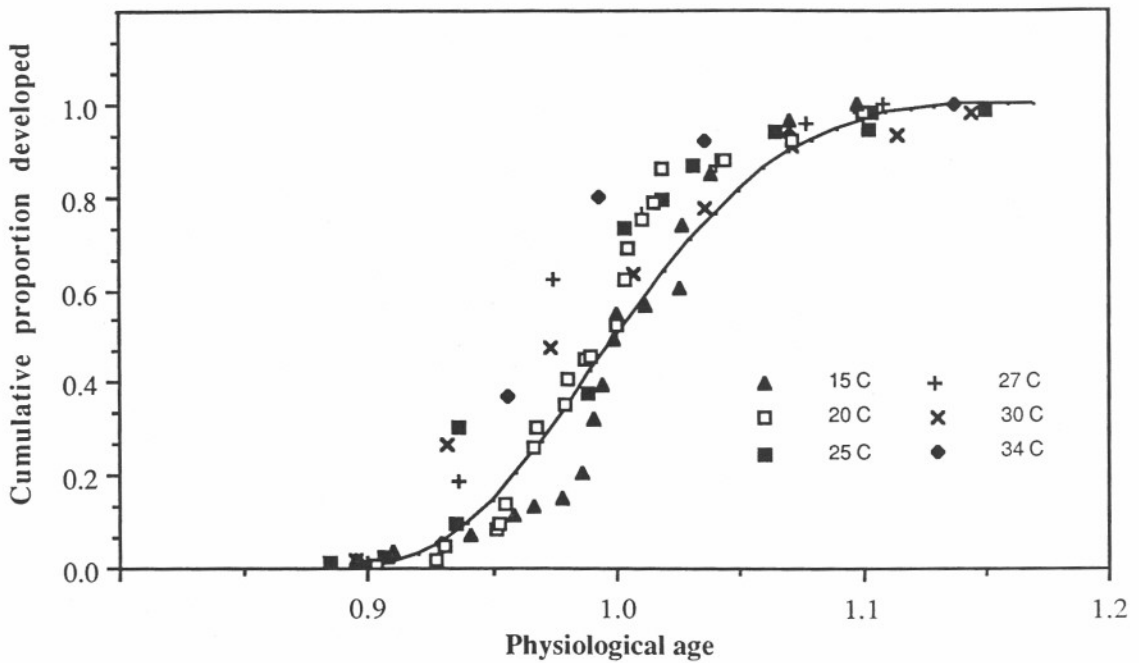
Fig. 1. Cumulative proportion of *Cx. quinquefasciatus* population completing development from egg hatch to adult emergence as a function of median physiological age. Line represents predicted distribution; points represent observed distribution at six temperatures.
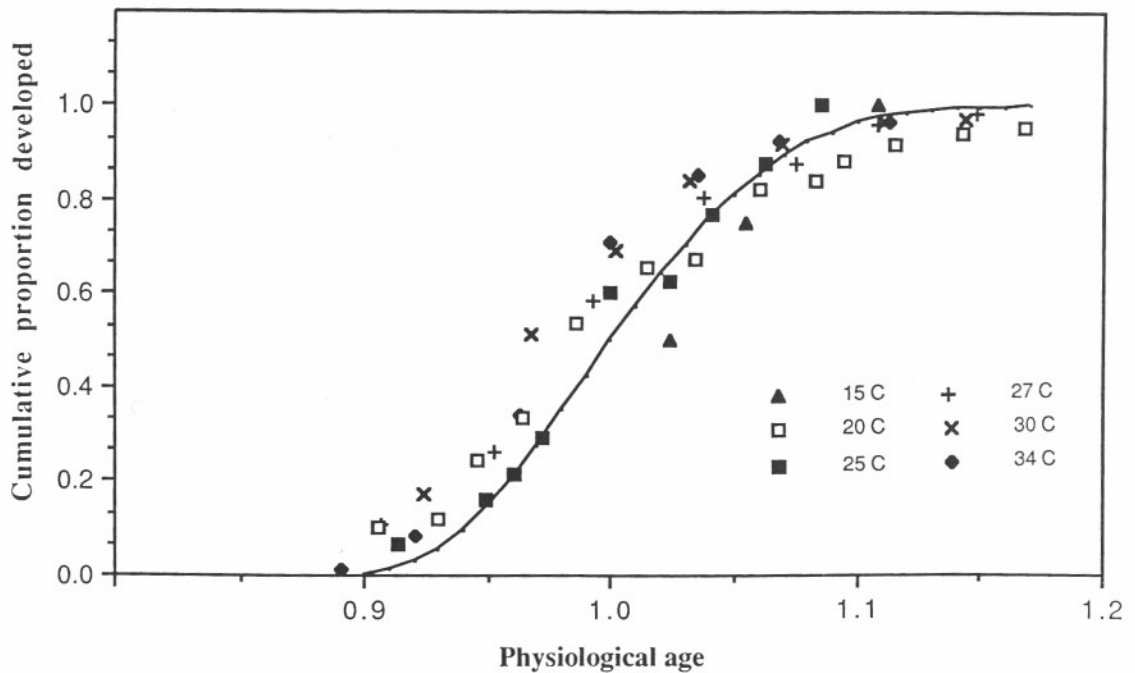

Fig. 2. Cumulative proportion of *Ae. aegypti* population completing development from egg hatch to adult emergence as a function of median physiological age. Line represents predicted distribution; points represent observed distribution at six temperatures.

Table 4. Mean widths (mm) of larval head capsule, larval body lengths (mm), and the larval, pupal, and adult body weights (mg) of *Cx. quinquefasciatus* reared at six constant temperatures

Life stage and parameter	Temp, °C					
	15	20	25	27	30	34
First instar						
Head width	0.33a	0.32ab	0.31b	0.31b	0.31b	0.31b
Second instar						
Head width	0.51a	0.51a	0.51a	0.51a	0.49b	0.50b
Body length	2.40a	2.29b	2.27b	2.28b	2.25b	2.19c
Body weight	0.65a	0.60ab	0.59ab	0.54b	0.54b	0.43c
Third instar						
Head width	0.82a	0.82a	0.78b	0.77bc	0.78b	0.76c
Body length	3.79a	3.73ab	3.68bc	3.72b	3.65c	3.63c
Body weight	1.23a	1.02ab	0.81b	0.71b	0.70b	0.69b
Fourth instar						
Head width	1.25a	1.21ab	1.18b	1.19b	1.17b	1.11c
Body length	5.71a	5.63ab	5.59ab	5.50b	5.33c	5.31c
Body weight	3.52a	2.89b	2.59b	2.74b	2.55b	2.45c
Pupa						
Body weight	5.77a	4.01bc	4.42b	3.68bc	3.46c	3.59c
Female adult						
Body weight	2.81a	1.64c	1.95b	2.17b	1.95b	1.95b
Male adult						
Body weight	2.10a	1.25d	1.74b	1.47c	1.35cd	1.73b
Combined adults						
Body weight	2.45a	1.45c	1.85b	1.82b	1.65bc	1.84b

Means followed by the same letter within rows are not significantly different ($P > 0.05$; Tukey's test [SAS Institute 1982]).

significant decrease, however, was recorded at 25–34°C. For the total developmental period and for other larval and pupal stadia, *Ae. aegypti* exhibited significant decreases similar to those for *Cx. quinquefasciatus*.

The percentages (and range) of total development time, over the entire range of temperatures, spent in each immature stage by *Cx. quinquefasciatus* were: 14% (11.9–18.4) for first stadium, 13% (10.1–14.5) for second stadium, 17% (14.7–20.4) for third stadium, 33% (27.3–37.9) for fourth stadium, and 23% (19.2–26.2) for the pupal stage. For *Ae. aegypti*, the percentages were: 19% (13.9–23.1) for first stadium, 14% (11.3–21.3) for second stadium, 17% (13.0–27.0) for the third stadium, 27% (24.2–28.5) for fourth stadium, and 23% (15.3–28.5) for the pupal stage.

The four-parameter Sharpe & DeMichele model (Equation 1) incorporating high-temperature inhibition described the temperature-dependent median development rates of both mosquito species very well (Table 3). The R^2 values ranged from 0.97 to 0.99 and from 0.95 to 0.98 for *Cx. quinquefasciatus* and *Ae. aegypti*, respectively. *Cx. quinquefasciatus* and *Ae. aegypti* reached maximum median development rates (days^{-1}) of 0.143 and 0.159, respectively, at 34°C.

The predicted (using the method of Stinner et al. 1975) and estimated cumulative proportion of individual mosquitoes completing development as a function of estimated physiological age are pre-

sented in Fig. 1 and 2. Inaccuracies in the estimation of developmental rates are expressed by any divergence of the observed data from the predicted curve. For example, in both species, the predicted total developmental rates were low at 15°C and slightly high at 25°C. In *Ae. aegypti*, only a few individuals were able to complete development at 15°C.

Published reports on development times for *Cx. quinquefasciatus* and *Ae. aegypti* do not present as detailed data for each larval instar and pupae as does our study; consequently, comparisons other than overall development times (egg to adult emergence) are difficult to make. In our study, developmental times for *Cx. quinquefasciatus* were longer than those reported by Shelton (1973) and Madder et al. (1983). For example, comparing our data for 15 and 20°C with those of Shelton (1973) for the period from first instar to adult emergence, our mean developmental times were about 19.8 and 4.1 d longer, respectively. Our mean developmental times for the same period and temperatures were about 4.3 and 0.5 d, respectively, longer than those observed by Madder et al. (1983). In *Ae. aegypti*, our mean development times at 20°C were about 5 d shorter than that reported by Bar-Zeev (1958). At 30 and 34°C, however, our development times were similar to those of Bar-Zeev (1958). These differences could be caused by single versus group rearing or by different strains of mosquitoes used in the studies. Variations in life table

Table 5. Mean widths (mm) of larval head capsule, larval body lengths (mm), and the larval, pupal, and adult body weights (mg) of *Ae. aegypti* reared at six constant temperatures

Life stage and parameter	Temp, °C					
	15	20	25	27	30	34
First instar						
Head width	0.28a	0.26b	0.26b	0.26b	0.25b	0.23c
Second instar						
Head width	0.47a	0.46ab	0.46ab	0.46ab	0.45b	0.44b
Body length	3.19a	3.19a	3.06b	2.92c	2.79d	2.80d
Body weight	0.74a	0.59b	0.56bc	0.49bcd	0.46cd	0.42d
Third instar						
Head width	0.75a	0.74ab	0.71bc	0.72b	0.69c	0.67d
Body length	4.43a	4.33a	4.34a	4.39a	4.36a	4.30a
Body weight	1.60a	1.64a	1.36b	1.34b	1.25b	1.09b
Fourth instar						
Head width	0.98a	0.99a	0.97a	0.93b	0.93b	0.92b
Body length	6.57a	6.47a	6.41a	6.44a	6.39ab	6.12b
Body weight	4.29a	4.21a	4.01ab	3.72ab	3.04bc	2.35c
Pupa						
Body weight	5.98a	5.76a	4.24b	4.03bc	3.95bc	3.20c
Female adult						
Body weight	—	2.07a	1.59b	1.19c	2.07a	1.65b
Male adult						
Body weight	—	1.29a	1.11b	0.76d	1.20a	0.93c
Combined adults						
Body weight	—	1.68a	1.35b	0.97c	1.64a	1.29b

Means followed by the same letter within rows are not significantly different ($P > 0.05$; Tukey's test [SAS Institute 1982]).

parameters among different strains of *Ae. aegypti* and *Cx. quinquefasciatus* have been reported by Crovello & Hacker (1972) and Walter & Hacker (1974), respectively, but their conclusions were based on data collected at only one temperature. Given the parameter values in Table 3, the Sharpe & DeMichele model may describe adequately the temperature-dependent development of other strains of these species and that could be verified by comparison with data on total development time collected at two or three temperatures. If necessary, the parameters could be changed to fit the data obtained with other strains more adequately.

Temperature affected the head capsule widths, body lengths, and weights in *Cx. quinquefasciatus* and *Ae. aegypti* (Tables 4 and 5). For both species, body size generally decreased as temperature increased. The head capsules of all instars in both species were significantly wider at 15 than at 30 and 34°C. Except for the third instar of *Ae. aegypti*, the larvae in both species were significantly longer at 15 than at 34°C. The body weights of all instars and pupae of both species, and the adult males and females of *Cx. quinquefasciatus*, were significantly greater at 15 than at 30–34°C. The inverse relationship between temperature and body size could possibly be the result of more rapid development at higher temperatures (Laudien 1973). The growth rate may increase with temperature, but the decrease in time available for growth has a greater

effect on the size. Thus, the resulting insect is smaller (McHugh & Olson 1982).

Both species developed to the adult stage at all constant temperatures tested (Table 6). In *Cx. quinquefasciatus*, survival to adult stage was significantly lower at 15 and 34°C than at 20–30°C. On the other hand, *Ae. aegypti* had significantly lower survival to adult stage at 15 than at 20–34°C, and its highest survival rate was recorded at 20 and 27°C. The proportion of the total mortality, averaged over all temperatures, which occurred during each immature stage differed for *Cx. quinquefasciatus* and *Ae. aegypti*, with about 15 and 78% for first instar, 13 and 9% for second instar, 6 and 7%

Table 6. Effect of constant temperatures on *Cx. quinquefasciatus* and *Ae. aegypti* survival from egg hatch to adult stage

Temp, °C	Mean (±SE) survival, %	
	Cx. quinquefasciatus	*Ae. aegypti*
15	38.15 (2.89)a	3.11 (1.33)a
20	85.25 (2.62)b	91.80 (3.05)c
25	90.30 (1.41)b	62.58 (2.49)b
27	84.87 (2.72)b	89.76 (3.75)c
30	83.12 (1.63)b	66.34 (2.74)b
34	42.07 (2.02)a	59.14 (3.08)b

Data subjected to arcsine transformation for analysis. Mean percentages in the same column followed by the same letter are not significantly different ($P > 0.05$; Tukey's test [SAS Institute 1982]).

for third instar, 21 and 4% for fourth instar, and 42 and 2% for pupal stage, respectively. For *Cx. quinquefasciatus*, high survival at midrange temperatures (20–30°C) was evident, with survival drastically decreasing above and below that range. A similar trend was observed by Shelton (1973) for this species. For *Ae. aegypti*, the lowest immature survival (3%) was observed at 15°C, whereas the highest survivals were at 20 (92%) and 27°C (90%). Bar-Zeev (1958) reported highest larval and pupal survival of *Ae. aegypti* at 20°C, but none survived at 14°C. The techniques used in our study apparently inflicted minimal mortality because survival to the adult stage at 20 and 30°C in *Cx. quinquefasciatus* and *Ae. aegypti* was greater than reported by Madder et al. (1983) and Bar-Zeev (1958), respectively.

Our data on temperature-dependent development, and our demonstration of the fit of the Sharpe & DeMichele model with appropriate parameters, provide a major component required for the development of simulation models for the population dynamics of these mosquito species. Obviously, the effects of other factors (e.g., food quality, water quality, light regimen, adult survival, and oviposition) in addition to temperature also must be included in such simulation models.

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