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ARTICLE

Temperature Effects on the Dynamics of *Aedes albopictus* (Diptera: Culicidae) Populations in the Laboratory

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ABSTRACT We investigated how constant temperatures of 22, 24, and 26°C experienced across the full life cycle affected the dynamics of caged populations of *Aedes albopictus* (Skuse). All cages were equipped with plastic beakers that served as sites for oviposition and larval development. We measured the per capita daily mortality and emergence rates of the adults and size of adult females, and estimated the intrinsic rate of increase (r) and asymptotic density (K) for each caged population. Populations at 26°C had greater intrinsic rates of increase and lower asymptotic densities than populations at 22 and 24°C. Populations at high temperatures initially had greater daily per capita emergence rates, and steeper declines in per capita emergence rate as density increased over the course of the experiment. There was no temperature effect on the size of adult females nor on the per capita daily mortality rate of adults. Results indicated that populations of *Ae. albopictus* occurring in regions with relatively high summer temperatures are likely to have high rates of population growth with populations of adults peaking early in the season. These populations may attain relatively low peak densities of adults. Populations occurring in regions with low summer temperatures are likely to experience slow, steady production of adults throughout the season with population size peaking later in the season, and may attain higher peak densities of adults. High temperature conditions, associated with climate change, may increase the rate of spread of *Ae. albopictus* by increasing rates of increase and by enhancing colonization due to rapid population growth.

KEY WORDS *Aedes albopictus*, rate of increase, asymptotic density, mortality rate, emergence rate, global climate change

Aedes albopictus (SKUSE) is an introduced container-dwelling mosquito native to Asia. Larvae develop in water-filled tires, cemetery vases, bird baths, other artificial containers, and tree holes. Females deposit desiccation resistant eggs on walls of containers, and these eggs hatch when flooded (Hawley 1988). *Aedes albopictus* is an ecological generalist adapted to both tropical and temperate climates and capable of using a wide range of suitable container habitats (Hawley 1988). Breeding populations of *Ae. albopictus* became established in the United States in the mid-1980s via imported used automobile tires (Hawley et al. 1987). Since its introduction, *Ae. albopictus* has spread rapidly and established breeding populations over much of the eastern United States.

Previous ecological research on *Ae. albopictus* has focused on diapause, freezing tolerance (Pumpuni et al. 1992, Focks et al. 1994, Hanson and Craig 1995), and its competitive interactions with other mosquitoes (Livdahl and Willey 1991, O'Meara et al. 1995, Juliano 1998). Few studies have focused on the effects of temperature during the active season on the life history traits (e.g., age at pupation, adult size, female fecundity) of this species (Hien 1975). In tropical and subtropical climates, *Ae. albopictus* is abundant year round; however, in temperate climates such as the midwestern United States and Japan, the active season for larval stages is limited to late spring through early fall, with larval abundance greatest in July–August (Mori and Wada 1978, Toma et al. 1982). *Aedes albopictus* occurs over a wide geographic range and encounters a wide range of ambient temperatures. The range expansion of *Ae. albopictus* in North America is likely to continue, and regional differences in temperature may affect its population dynamics, as is the case in other mosquitoes (e.g., Rueda et al. 1990, Lyimo et al. 1992).

In addition to encountering regional differences in temperature as a result of its spread in North America, *Ae. albopictus* is likely to be affected by climate change. Human activities, mainly the burning of fossil fuels, have added large amounts of greenhouse gases (e.g., CO_2, CH_4, O_3, NO) to the atmosphere (Vitousek 1994, Patz et al. 1996), which enhance the greenhouse effect. These atmospheric changes are likely to have major climatic consequences, such as predicted increases in global average temperature of 1.5–4.5°C if greenhouse gases double in the next century (Schneider 1993). For *Ae. albopictus*, such temperature changes may affect population dynamics by altering reproductive and mortality rates (Porter et al. 1991, Lawton 1995, Sutherst et al. 1995), and therefore may affect its range expansion.

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Although it is likely that different temperatures affect the population dynamics of *Ae. albopictus*, the specific direction of that effect is difficult to predict. Increased temperatures, up to a point, are likely to increase *Ae. albopictus* population growth by increasing growth and development rates (e.g., Hien 1975). However, increased temperatures also are likely to be associated with greater desiccation, perhaps causing greater mortality of egg or adult *Ae. albopictus* (Sota and Mogi 1992a, 1992b; Reeves et al. 1994; Mogi et al. 1996), which may have important consequences for the spread of this species. Many investigations of temperature effects on mosquitoes have focused on only part of their life cycle, mainly aquatic stages (e.g., Hien 1975, Rueda et al. 1990). Temperature may affect egg viability (e.g., Parker 1986), larval development (e.g., Rueda et al. 1990), blood-feeding behavior (e.g., Crans et al. 1996), female fecundity (e.g., Hurlbut 1973), and adult longevity (e.g., Hawley 1985, Day et al. 1990), influencing populations in uncertain ways. For example, individuals reared at higher temperatures may develop more rapidly, but these adults tend to be smaller (Day et al. 1990, Rueda et al. 1990). Female size is positively related to fecundity (Steinwascher 1982, Day et al. 1990). How such effects of rearing temperature on mortality, development rate, and adult size combine to affect population growth cannot be determined without experiments.

The current study investigates how constant temperature across the entire life cycle affects the population dynamics of *Ae. albopictus.* This experiment will provide information relevant to predicting how regional differences in summer temperature within eastern North America and possible increases in temperature due to climate change may affect the range expansion of *Ae. albopictus.*

Materials and Methods

Source of Mosquitoes. *Aedes albopictus* eggs used in this experiment were the offspring of field-collected mosquitoes from east St. Louis, IL. It is likely that this source population is the strain of *Ae. albopictus* currently undergoing expansion in the midwestern United States. Field-collected *Ae. albopictus* were allowed to mate freely in 0.6-m^3 cages at a photoperiod of 16:8 (L:D) h and 22–27°C. This colony was blood fed weekly on anesthetized laboratory mice (Illinois State University Animal Care protocol 1-98-06) and provided with ≈ 10% sucrose solution ad libitum (Munstermann and Wasmuth 1985, Juliano 1989, Juliano et al. 1993).

Experimental Design and Data Collection. Experimental containers, used for oviposition and larval development, consisted of 500-ml plastic beakers lined with durable paper and filled with 400 ml of a 2:1 mixture of tire and deionized water. Black locust (*Robinia psuedoacacia* (L.) leaves (2.00 ± 0.05 g dry mass after 24 h at 60°C) and fine particulate sediment from tires (1 g autoclaved drained fresh mass) were added to each beaker. Tire water, sediment, and leaves were collected from an established tire site near Normal, IL. Tire water was filtered through a 70-μm filter to remove unwanted organisms while allowing microbes to pass. After the contents of the beakers had soaked for 10 d, *Ae. albopictus* F_1 eggs were synchronously hatched (Novak and Shroyer 1978), and 50 F_1 first instars (<24 h old) were added to each of the beakers. Two beakers were placed in each of nine experimental cages, each constructed from a 20-liter plastic bucket equipped with a cloth sleeve and a 0.5-mm nylon mesh top allowing for air flow and evaporation. The cages provided an environment suitable for completion of the entire life cycle of *Ae. albopictus.* Water within the beakers was allowed to evaporate to 90% of its maximum volume of 400 ml, then returned to 400 ml using deionized water. These water additions simulated episodic rainfall and induced hatches of eggs and subsequent cohorts of larvae in beakers. All cages were continuously provided with ≈10% sucrose solution and weekly blood meals from anesthetized laboratory mice, using methods similar to those for the parental generation. The experiment ran for 120 d, which was long enough for the production of several generations of adults. Cages were placed in environmental chambers (Percival I-35VL, Boone, IA) set at constant temperatures of 22°C, 24°C, and 26°C and a photoperiod of 16:8 (L:D) h. These temperatures approximated the range of mean July temperatures between 39 and 41° N latitude in the midwestern United States, respectively (Court 1974), areas recently invaded by populations of *Ae. albopictus* during its current range expansion. The 4°C temperature range we used also approximated the predicted increase in temperatures due to anthropogenic climate change (Schneider 1993). We maintained three replicates at each temperature (3 cages per environmental chamber, nine total cages). In this experiment, humidity within environmental chambers was not controlled; however, a 2-wk monitoring period (seven readings) at the start of the experiment indicated that humidity was relatively high and fairly constant among temperatures (79.17 ± 0.48%–85.71 ± 0.29%, mean ± SE relative humidity using humidity pens (Fisher, Fairlawn, NJ).

When the first pupae appeared, beakers within the cages were checked daily and pupal exuviae were removed, examined at 16× magnification to determine sexes, and emergence enumerated by date. Similarly, we determined mortality by daily removal of dead adults within the cages, and recorded escaped adults (which were killed and counted as mortality). It is likely that a small number of pupal exuviae, escaped adults, and dead adults were not recorded. However, a comparison of the actual versus estimated number of adults remaining at the end of the experiment showed that estimates were within 15% (average deviation) of the actual number of adults remaining. Four of the caged populations yielded overestimates of the number of adults, and four caged populations yielded underestimates, with no apparent trend among temperatures. Therefore, our methods for recording emergence and mortality were unbiased and relatively accurate. We determined the mean size of adult females by measuring wing lengths of females (dried for

24 h 60°C) from the beginning ($n = 10$) and end ($n = 10$) from each cage.

Data and Analyses. In one replicate at 26°C, all larvae died within the first week; therefore, no adults were produced. This replicate was excluded from analysis. For all variables, temperature effects were analyzed by one-way analyses of variance ANOVA (SAS Institute 1989) and randomization ANOVA (RT version 1.02, Manly 1991a, 1991b). Because of the relatively small sample size, a deviation from normality may go undetected. Therefore, randomization ANOVAs (which do not assume normality) served as a check on the sensitivity of results to any departure from normality. For all analyses, except intercept estimates for the emergence rate, we could not reject null hypotheses of normality (Kolmogorov–Smirnov test) and homogeneous variances (Levene's test) for the raw data. Intercept estimates for the emergence rate were transformed reciprocally to meet the assumptions. For all analyses, results from standard and randomization ANOVAs were similar, and only results of standard ANOVAs are reported. When a significant temperature effect was detected, we compared all possible pairs of treatment means at an experimentwise $\alpha = 0.05$ (Ryan-Einot-Gabriel-Welsch multiple range test; SAS Institute 1989).

Population Growth. For each cage we estimated the number of adults alive on each day (t) by determining daily number of newly emerged adults (B_t) (based on exuviae recovered), and daily number of deaths of adults (D_t) (escapes and recovered dead bodies). On any day, the number of adults alive (N_t) was simply $N_{t-1} + B_t - D_t$ (Fig. 1). Intrinsic rate of increase (r) and asymptotic density (K) for the adult population were determined for each replicate cage using the logistic growth equation:

$$N_t = \left[\frac{K}{1 + [(K - N_0)/N_0]e^{-rt}} \right], \qquad [1]$$

where N_t is the number of adults alive on day t_{1-120}, K is the asymptotic density for the adult population in the cage, r is the intrinsic rate of increase for the adult population in the cage, N_o is the initial number of adults at the start of the experiment, and t ranges from 1 to 120 d. We set $N_o = 1$ which is equivalent to assuming that one female laid the eggs that produced the 100 first instars added to the cage (i.e., 50 per beaker). This offspring number is greater than the typical fecundity values for the first gonotrophic cycle of *Ae. albopictus* (42–88 eggs per blood meal, Hawley 1988), but it is well within egg counts observed for individuals in the laboratory (S.A.J., unpublished data). We used nonlinear regression (SAS Institute 1989, PROC NLIN; Juliano 1993) to estimate r and K for each cage. For this analysis, our goal was not tests of whether r and K for individual cages were significantly different from 0. Rather, we were interested in how temperature affected mean r and K for the replicate cages. A one-way ANOVA with temperature as a categorical variable was used to test for temperature effects on estimates of r and K from experimental cages.

Typically, calculations of the intrinsic rate of increase (r) and carrying capacity (K) in a limited environment assume that nothing is added or subtracted from the environment except food resources. This eliminates the possibility that a population fails to reach its carrying capacity due to resource limitation (e.g., Brower et al. 1990). A population that reaches its carrying capacity is assumed to be in a state of equilibrium (i.e., births = deaths). Alternatively, in some systems, resources are nonrenewable (e.g., space). In these systems the concept of carrying capacity takes on a different meaning. Carrying capacity is reached after all available resources have been exhausted (e.g., Ricklefs 1984). In our experiment, we added larval food resources only at the start of the experiment. Therefore, it is likely that populations did not reach a state of equilibrium with their resources. Therefore, K should be thought of as asymptotic or maximal density of adults attained before a decline in the population due to resource limitation.

Mortality and Emergence Rates. For all caged populations, there was a distinct gap of several days between emergence of the F_1 and F_2 cohorts. During this time, very few or no adults emerged, and F_2 eggs, larvae, and pupae were developing. For each replicate cage, we determined per capita daily mortality and emergence rates of adults (sexes pooled) for the interval from the start of emergence of the F_2 cohort to the day on which N_t was maximal. Per capita mortality was calculated as the daily sum of dead and escaped adults divided by the number of adults alive on the previous day. Per capita daily emergence rate was calculated as the daily sum of new adults from both beakers, divided by the number of adults alive from the previous day.

We first tested whether per capita daily emergence and mortality rates for each cage were density dependent by fitting an autoregressive time series model (SAS Institute 1989, PROC AUTOREG, Rasmussen et al. 1993) to data on rate versus density of adults (N_t). For the emergence rate, it would have been ideal to use density of larvae rather than density of adults in this regression; however, the design of this study precluded daily counts of larvae in beakers, so for analysis of density dependent emergence, we assumed that the only daily estimate of abundance at our disposal, N_t, provided an index of the unmeasured density of larvae. We fit autoregressive models for the period from the start of emergence of the second cohort to the day on which N_t was maximal. Autoregressive time series models are a subset of time series analyses and are used for analyzing time-ordered sequences of observations in which observations at one time period depend in some way on previous observations (Rasmussen et al. 1993). The main virtue of these models is that they provide unbiased estimates of slopes of regressions when there is serial autocorrelation among observations (Neter and Wasserman 1974, SAS Institute 1989). In an autoregressive model, the value of an

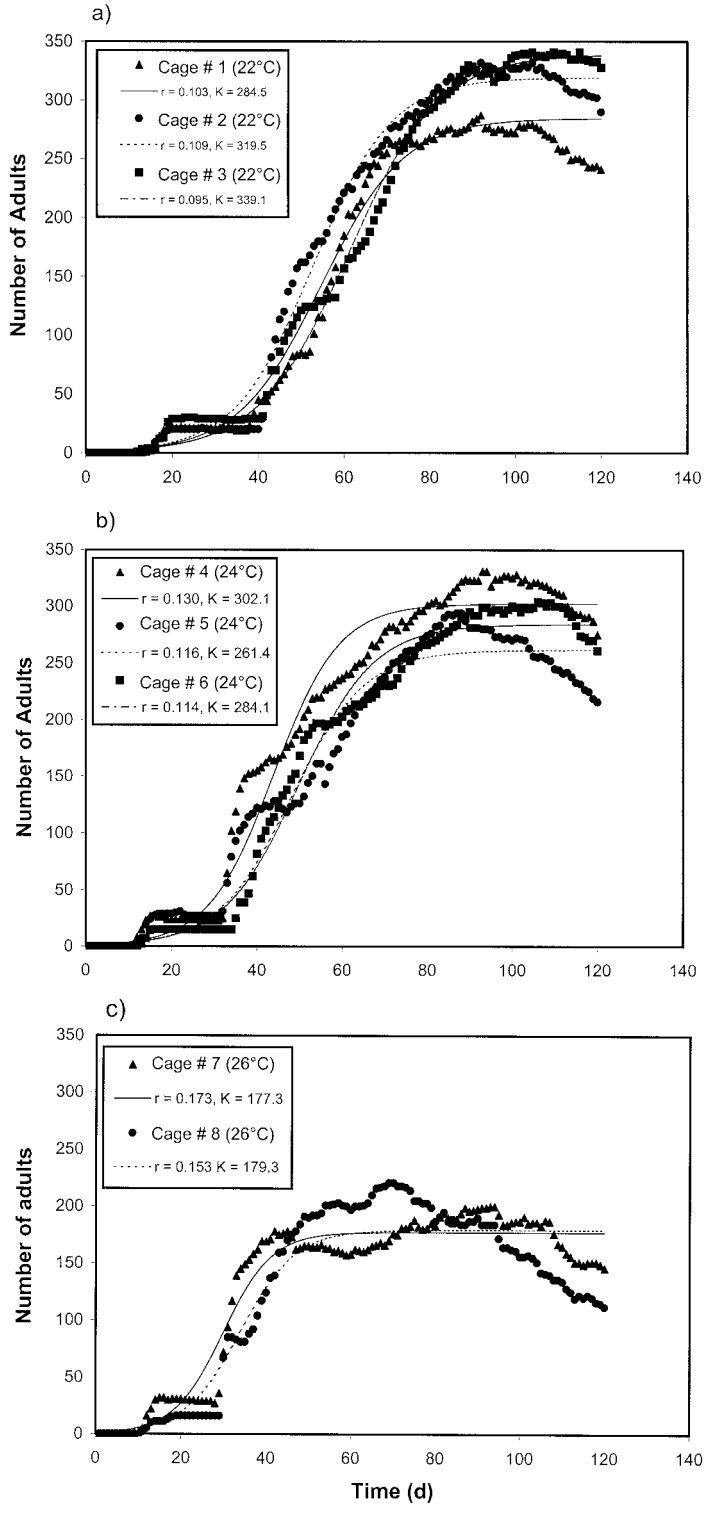

Fig. 1. Estimated number of adults based on daily emergences and daily adult mortality in each population at (a) 22°C, (b) 24°C, and (c) 26°C. Intrinsic rate of increase (r) and asymptotic density (K) for the adult population were determined for each cage using the logistic growth equation.

observed variable at time t (y_t) is a linear function of previous values (e.g., y_{t-1}, y_{t-2}, y_{t-3}):

$$y_t = \phi_1 y_{t-1} + \phi_2 y_{t-2} + \phi_3 y_{t-3} + \ldots + \varepsilon_t, \quad [2]$$

where ε_t is random error at time t, with mean = 0 and standard deviation = σ. The coefficients ϕ are analogous to regression slopes, but define the relationship between y values at time t and y values some number of time units in the past (Rasmussen et al. 1993). In our data set, y values are per capita mortality or emergence rates determined each day (t). We were interested in whether there was any relationship between y_t and the density recorded at time t (N_t), so that the model becomes:

$$y_t = \alpha + \beta N_t + \phi_1 y_{t-1} + \phi_2 y_{t-2} + \phi_3 y_{t-3} + \ldots + \varepsilon_t, \quad [3]$$

where β is the slope of the regression of per capita mortality (y_t) versus density (N_t) and α is the intercept. Our goal was to test significant relationships between per capita mortality or emergence rates and density that were not biased by autocorrelation (Neter and Wasserman 1974). We tested for significant autocorrelation for observations 1–14 d before the current observation.

Development Time and Size. Mean times to emergence for males and females of the first cohort were determined for each replicate cage. We determined the mean size of adult females from a cage at the beginning and end of the experiment. The first 10 females that died in each cage represent the 'beginning' and a random sample of females remaining after 120 d were used for the 'end.' Wing lengths from the beginning also were compared with those from the end for each cage. Wing length was determined by the distance from the proximal edge of the costa to the distal end of the R_2 vein (adults dried for ≥24 at 60°C). When both wings of an individual were available, we used the average length of the two wings. Wing lengths were measured by a computer imaging system using Image-Pro Plus software (Media Cybernetics, L.P., Silver Spring, MD, version 3.0, 1993–1997).

Results

The cumulative amount of water added to beakers did not differ significantly among the temperature treatments ($F = 0.91$; df = 2, 5; $P = 0.4591$; mean ± SE: 22°C = 826.7 ± 35.3 ml, 24°C = 893.3 ± 70.6 ml, 26°C = 940.0 ± 60.0 ml). There was an average of 22 water additions to each replicate cage (i.e., water added to either beaker) over the 120 d of the experiment.

Population Growth. Temperature significantly affected r ($F = 24.50$; df = 2, 5; $P = 0.0026$), with 26°C having the greatest r relative to 22 and 24°C for the adult populations (Fig. 2a). Temperature also significantly affected K ($F = 24.52$; df = 2, 5; $P = 0.0026$), with populations at 26°C attaining a significantly lower K compared with the other two temperatures (Fig. 2b).

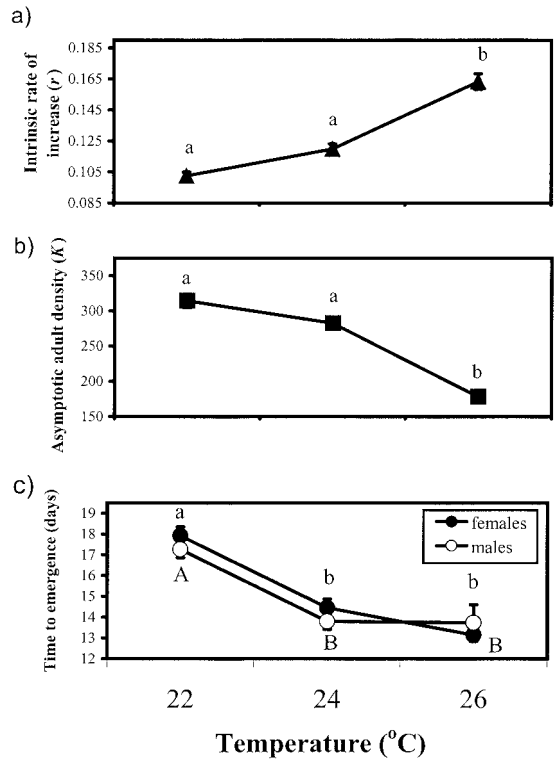

Fig. 2. Means ± SE for intrinsic rate of increase (r), asymptotic densities (K), and time to emergence for females and males of the first cohort for the adult populations at 22, 24, and 26°C. Means of temperature treatments followed by the same letter are not significantly different. Points lacking error bars indicate standard errors that were too small to appear on the graph.

Mortality and Emergence Rates. For the mortality rates, autocorrelations were significant in only two of the cages, and, more importantly, we found no significant relationship between per capita adult mortality and density (Table 1). Therefore, mortality rate appeared to be density independent, so we estimated the overall mortality rate for a cage as the mean across all days, and tested for temperature effects on these mean daily mortality rates. For the per capita emergence rate, autocorrelations were significant (six of eight cages) and, more importantly, the per capita emergence rate decreased significantly with density of adults (Table 1). Therefore, the emergence rate of adults was density dependent, and we analyzed the temperature effect on the emergence rate by one-way ANOVAs on the slopes and intercepts for emergence rate versus adult density estimated for each cage from the autoregressive time series models.

Mortality rate of adults was not significantly affected by temperature ($F = 1.11$; df = 2, 5; $P = 0.4003$) (Table 2). Temperature significantly affected estimates of slopes ($F = 128.12$; df = 2, 5; $P = 0.0001$) and intercepts ($F = 63.06$; df = 2, 5; $P = 0.0003$) from the autoregressive model of daily emergence rate against adult density. Higher temperatures yielded steeper

Table 1. Estimated slopes from the autoregression analysis that relate per capita rates of emergence and mortality of adults to density of adults for 22, 24, and 26°C

Temp, °C	Cage	Per capita emergence rate				Per capita mortality rate			
		Slope	*F*	df	*P*	Slope	*F*	df	*P*
22	1	−0.0004	11.75	1, 58	0.0011	−0.000002	0.01	1, 58	0.9088
	2	−0.0003	4.99	1, 64	0.0289	−0.000003	0.06	1, 64	0.8145
	3	−0.0003	10.98	1, 66	0.0015	0.000017	2.59	1, 66	0.1122
24	4	−0.0014	14.58	1, 60	0.0003	−0.000026	1.13	1, 60	0.2929
	5	−0.0008	13.64	1, 54	0.0005	−0.000069	2.16	1, 54	0.1472
	6	−0.0010	59.82	1, 70	<0.0001	0.000008	0.22	1, 70	0.6377
26	7	−0.0036	62.90	1, 63	<0.0001	−0.000043	0.39	1, 63	0.5371
	8	−0.0033	5.87	1, 38	0.0202	−0.000021	0.24	1, 38	0.6291

negative slopes (i.e., more rapid decline of emergence rate with density) and higher *y*-intercepts (i.e., greater initial emergence rates). All three temperature treatments were significantly different from one another (Table 2).

Development Time and Size. Mean time to emergence for the first cohort was significantly affected by temperature for both males ($F = 17.02$; df = 2, 5; $P = 0.0059$) and females ($F = 33.81$; df = 2, 5; $P = 0.0012$) with both sexes developing significantly more slowly at 22°C compared with 24°C and 26°C (Fig. 2c). Size of adult females either at the beginning ($F = 0.37$; df = 2, 5; $P = 0.7078$) or end ($F = 1.44$; df = 2, 5; $P = 0.3205$) of the experiment was not significantly affected by temperature (Table 2). There was a significant decline in size of females from beginning to end ($F = 26.27$; df = 1,7; $P = 0.0014$; Table 2), but the decline in size did not differ significantly among temperatures ($F = 0.30$; df = 2, 5; $P = 0.7529$; Table 2).

Discussion

Our results clearly show that temperature affects the population dynamics of *Ae. albopictus.* Populations at 26°C had greater intrinsic rates of increase (r) and lower asymptotic densities (K) relative to populations at the other two temperatures (Figs. 2a and 2b). Greater intrinsic rate of increase (r) at 26°C could result if the adult emergence rate increased and larval development time decreased with increased temperatures. Lower K at 26°C could result if populations at 26°C had greater daily mortality rates of adults, and thus lower asymptotic densities, or resource depletion and limitation in the aquatic habitats progressed more rapidly at 26°C, resulting in a steeper decrease in the emergence rate with density of adults at the higher temperature.

Populations at 24 and 26°C did yield shorter development times for emergence of the first cohort (Fig. 2c). Also, we detected a significant temperature effect on slope and intercept estimates for the regression of per capita daily emergence rate against adult density. We were unable to detect any temperature effects on mean daily mortality rates of adults (Table 2), and mortality appeared to be density independent. Several authors have noted that death rates of adults are unlikely to be density dependent in nature as well (e.g., Service 1985, Charlwood et al. 1995).

In this experiment, decaying plant material that served as the resource base for larvae was added only once. This simulates container habitats in the temperate zone, which receive leaf inputs primarily during autumn. It is likely that resource depletion and limitation for larvae became more important as the experiment progressed because of depletion of resources added at the beginning (Gee 1988, Richardson 1991). Rate of decay of leaf litter within containers, and associated growth of microbial populations, which are the actual food for *Aedes* (Fish and Carpenter 1982), may have increased with temperature, as observed in other aquatic systems (Paul et al. 1978, Carpenter and Adams 1979, Brock 1984). Therefore, it is possible that greater microbial growth at 26°C contributed to the observed greater intrinsic rate of increase (r) at 26°C. Additional experiments are needed to evaluate whether or not rate of leaf decay and microbial growth do in fact contribute to the temperature effects on *Ae. albopictus* population growth.

In our experiment, we expected higher temperatures to yield smaller females, as in previous studies

Table 2. Treatment means ±SE for mortality rate, emergence rate, and size of adult females at the beginning and end of the experiment

	22°C (n = 3 cages)	24°C (n = 3 cages)	26°C (n = 2 cages)
Mortality rate (adults/adult/d)	0.0087 ± 0.0011a	0.0114 ± 0.0016a	0.0124 ± 0.0031a
Slope: Emergence rate (adults/adult/d)	−0.0003 ± 0.00003a	−0.0011 ± 0.00017b	−0.0035 ± 0.00017c
Intercept: Emergence rate (adults/adult/d)	0.1174 ± 0.0019a	0.2910 ± 0.0531b	0.6580 ± 0.0010c
Female wing length (beginning), mm	2.63 ± 0.09a	2.58 ± 0.05a	2.53 ± 0.14a
Female wing length (end), mm	2.36 ± 0.08a	2.32 ± 0.08a	2.14 ± 0.10a

Treatment means ±SE for regression estimates of slopes and intercepts for per capita daily emergence rate versus adult density over the period from first emergence of the second cohort to the day on which maximum number of adults was attained. Means for a variable associated with the same letter are not significantly different (Ryan-Einot-Gabriel-Welsch multiple range test $\alpha = 0.05$; SAS Institute 1989).

(Day et al. 1990, Rueda et al. 1990). However, we did not detect any temperature effects on the size of females. This may be due to lack of statistical power because of small sample size or using a limited range of temperatures. Therefore, lack of an effect on size indicates that size-dependent female fecundity should be similar for these temperatures. Our data also indicated no effect of temperature on adult mortality, implying that temperature effects on fecundity via longevity of females were not present. We cannot rule out other temperature effects on female fecundity, such as more effective blood-feeding at greater temperatures (Hurlbut 1973, Crans et al. 1996), because we have no data on blood-feeding effectiveness.

Results from our study may have important implications for the current and future distribution of *Ae. albopictus* in North America. Although temperature effects on r and K from this experiment are unlikely to be quantitatively accurate predictors of r and K in natural populations, they may serve as useful indicators of trends in r and K with ambient temperature in nature. Populations of *Ae. albopictus* occurring in warmer temperate regions (e.g., southern United States) are likely to have greater intrinsic rates of increase (r) and lower asymptotic densities (K). These populations may be expected to peak early in the season and to attain a relatively low peak density of adults. In contrast, populations in cooler temperate regions (e.g., northern United States) are likely to have slower population growth, but more steady production of adults throughout the active season, and may attain greater peak densities. Temperature effects on r may have the greatest consequences for spread of *Ae. albopictus* in temperate regions with different temperatures. Population dynamic theory (e.g., MacArthur and Wilson 1967, Ebenhard 1991, Hanski 1999) predicts that probability of successful colonization of an empty site increases with increasing r, because rapid population increase enables a colonizing population to grow quickly beyond the small population sizes that render it vulnerable to stochastic extinction. Based on this theory, we would expect the spread of *Ae. albopictus* to new sites to be slowed in northern temperate regions by cooler summer temperatures associated with increasing latitude. Additional factors, such as patterns of precipitation, winter temperatures and their effects on population survival, and season length also may influence regional differences in the dynamics and spread of *Ae. albopictus* (Hawley 1985, Pumpuni et al. 1992, Washburn and Hartmann 1992, Focks et al. 1994, Hanson and Craig 1995).

Increased temperature associated with climate change, when considered alone, seems likely to expand the region of North America that is suitable for *Ae. albopictus.* Warmer winter temperatures should reduce winter mortality (Pumpuni et al. 1992, Focks et al. 1994, Hanson and Craig 1995). Warmer summer temperature should favor earlier, more rapid production of adults, and yield an increase in the rate of spread of *Ae. albopictus* to new sites by increasing r, and thus increasing the likelihood of successful colonization. Because effects of climate change will include changes in humidity and precipitation (Nawrocki and Hawley 1987, Schneider 1993, Vitousek 1994), in addition to changes in temperature, these predictions concerning spread of *Ae. albopictus* must be viewed as preliminary. Humidity and the pattern and amount of precipitation also play important roles in population dynamics of mosquitoes (e.g., Moore 1985), and are likely to interact with temperature in their effects on population dynamics. Furthermore, patterns of precipitation and temperature covary in nature. Accurate predictions of the effect of current and future climate on population dynamics and spread of *Ae. albopictus* will require experimental evaluation of multiple environmental factors on the entire life cycle of this species.

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References Cited

Brock, Th.C.M. 1984. Aspects of the decomposition of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Aquat. Bot. 19: 131–156.

Brower, J. E., J. H. Zar, and C. N. von Ende. 1990. Field and laboratory methods for general ecology. Wm. C. Brown, Dubuque, IA.

Carpenter, S. R., and M. S. Adams. 1979. Effects of nutrients and temperature on decomposition of *Myriophyllum spicatum* L. in a hard-water eutrophic lake. Limnol. Oceanogr. 24: 520–528.

Charlwood, J. D., T. Smith, J. Kihonda, B. Heiz, P. F. Billingsley, and W. Takken. 1995. Density independent feeding success of malaria vectors (Diptera: Culicidae) in Tanzania. Bull. Entomol. Res. 85: 29–35.

Court, A. 1974. The climate of the conterminous United States, pp. 193–344. *In* R. A. Bryson and F. K. Hare [eds.], Climates of North America, vol. 11. World Survey of Climatology. Elsevier, New York.

Crans, W. J., D. A. Sprenger, and F. Mahmood. 1996. The blood-feeding habits of *Aedes sollicitans* (Walker) in relation to Eastern Equine Encephalitis virus in coastal areas of New Jersey, II. Results of experiments with caged mosquitoes and the effects of temperature and physiological age on host selection. J. Vector Ecol. 21: 1–5.

Day, J. F., A. M. Ramsey, and J. Zhang. 1990. Environmentally mediated seasonal variation in mosquito body size. Environ. Entomol. 19: 469–473.

Ebenhard, T. 1991. Colonization in metapopulations: a review of theory and observations. Biol. J. Linn. Soc. 42: 105–121.

Fish, D., and S. R. Carpenter. 1982. Leaf litter and larval mosquito dynamics in tree-hole ecosystems. Ecology 63: 283–288.

Focks, D. A., S. B. Linda, G. B. Craig, W. A. Hawley, and C. P. Pumpuni. 1994. *Aedes albopictus* (Diptera: Culicidae): a statistical model of the role of temperature, photoperiod, and geography in the induction of egg diapause. J. Med. Entomol. 31: 278–286.

Gee, J.H.R. 1988. Population dynamics and morphometrics of *Gammarus pulex* L.: evidence of seasonal food limitation in a freshwater detritivore. Freshw. Biol. 19: 333–343.

Hanski, I. L. 1999. Metapopulation ecology. Oxford University Press, Oxford.

Hanson, S. M., and G. B. Craig, Jr. 1995. Relationship between cold hardiness and supercooling point in *Aedes albopictus* eggs. J. Am. Mosq. Control Assoc. 11: 35–38.

Hawley, W. A. 1985. The effect of larval density on adult longevity of a mosquito, *Aedes sierrensis:* epidemiological consequences. J. Anim. Ecol. 54: 955–964.

Hawley, W. A. 1988. The biology of *Aedes albopictus.* J. Am. Mosq. Control Assoc. 4(suppl): 1–40.

Hawley, W. A., P. Reiter, R. S. Copeland, C. B. Pumpuni, and G. B. Craig, Jr. 1987. *Aedes albopictus* in North America: probable introduction in used tires from Northern Asia. Science 236: 1114–1116.

Hien, D. S. 1975. Biology of *Aedes aegypti* (L., 1762) and *Aedes albopictus* (Skuse, 1865) (Diptera, Culicidae). Acta Parasitol. Pol. 23: 553–568.

Hurlbut, H. S. 1973. The effect of environmental temperature upon the transmission of St. Louis encephalitis virus by *Culex pipiens quinquefasciatus.* J. Med. Entomol. 10: 1–12.

Juliano, S. A. 1989. Geographic variation in vulnerability to predation and starvation in larval treehole mosquitoes. Oikos 56: 99–108.

Juliano, S. A. 1993. Nonlinear curve fitting: predation and functional response curves, pp. 159–182. *In* S. M. Scheiner and J. Gurevitch, [eds.], Design and analysis of ecological experiments. Chapman & Hall, New York.

Juliano, S. A. 1998. Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition. Ecology 79: 255–268.

Juliano, S. A., L. J. Hechtel, and J. R. Waters. 1993. Behavior and risk of predation in larval tree hole mosquitoes: effects of hunger and population history of predation. Oikos 68: 229–241.

Lawton, J. H. 1995. The response of insects to environmental change, pp. 4–22. *In* R. Harrington and N. E. Stork [eds.], Insects in a changing environment: 17th Symposium of the Royal Entomological Society, 7–10 September 1993. The Royal Entomological Society, London.

Livdahl, T. L., and M. S. Willey. 1991. Prospects for invasion: competition between *Aedes albopictus* and native *Aedes triseriatus.* Science 253: 189–191.

Lyimo, E. O., W. Takken, and J. C. Koella. 1992. Effect of rearing temperature and larval density on larval survival, age at pupation and adult size of *Anopheles gambiae.* Entomol. Exp. Appl. 63: 265–271.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Manly, B.F.J. 1991a. Randomization and Monte Carlo methods in biology. Chapman & Hall, London.

Manly, B.F.J. 1991b. RT: a program for randomization testing. Version 1:02. West Incorporated, Cheyenne, WY.

Mogi, M., I. Miyagi, K. Abadi, and Syafruddin. 1996. Inter- and intraspecific variation in resistance to desiccation by adult *Aedes* (*Stegomyia*) spp. (Diptera: Culicidae) from Indonesia. J. Med. Entomol. 33: 53–57.

Moore, C. G. 1985. Predicting *Aedes aegypti* abundance from climatological data, pp. 223–235. *In* L. P. Lounibos, J. R. Rey, and J. H. Frank [eds.], Ecology of mosquitoes: proceedings of a workshop. Florida Medical Entomology Laboratory, Vero Beach, FL.

Mori, A., and Y. Wada. 1978. The seasonal abundance of *Aedes albopictus* in Nagasaki. Trop. Med. 20: 29–37.

Munstermann, L. E., and L. M. Wasmuth. 1985. *Aedes triseriatus,* pp. 15–24. *In* P. Singh and R.F. Moore [eds.], Handbook of insect rearing, vol. 2. Elsevier, Amsterdam.

Nawrocki, S. J., and W. A. Hawley. 1987. Estimation of the northern limits of distribution of *Aedes albopictus* in North America. J. Am. Mosq. Control Assoc. 3: 314–317.

Neter, J., and W. Wasserman. 1974. Applied linear statistical models. Regression, analysis of variance, and experimental designs. Irwin, Homewood, IL.

Novak, R. J., and D. A. Shroyer. 1978. Eggs of *Aedes triseriatus* and *A. hendersoni:* a method to stimulate optimal hatch. Mosq. News 38: 515–521.

O'Meara, G. F., L. F. Evans, A. D. Getman, Jr., and J. P. Cuda. 1995. Spread of *Aedes albopictus* and decline of *Ae. aegypti* (Diptera: Culicidae) in Florida. J. Med. Entomol. 32: 554–562.

Parker, M. B. 1986. Hatchability of eggs of *Aedes taeniorhynchus* (Diptera: Culicidae): effects of different temperatures and photoperiods during embryogenesis. Ann. Entomol. Soc. Am. 79: 925–930.

Patz, J. A., P. R. Epstein, T. A. Burke, and J. M. Balbus. 1996. Global climate change and emerging infectious diseases. JAMA 275: 217–223.

Paul, R. P., E. F. Benfield, and J. Cairns. 1978. Effects of thermal discharge on leaf decomposition in a river ecosystem. Verh. Int. Verein. Limnol. 20: 1759–1766.

Porter, J. H., M. L. Parry, and T. R. Carter. 1991. The potential effects of climatic change on agricultural insect pests. Agric. For. Meteorol. 57: 221–240.

Pumpuni, C. B., J. Knepler, and G. B. Craig, Jr. 1992. Influence of temperature and larval nutrition on the diapause inducing photoperiod of *Aedes albopictus.* J. Am. Mosq. Control Assoc. 9: 223–227.

Rasmussen, P. W., D. M. Heisey, E. V. Nordheim, and T. M. Frost. 1993. Time-series intervention analysis: unreplicated large-scale experiments, pp. 138–158. *In* S. M. Scheiner and J. Gurevitch [eds.], Design and analysis of ecological experiments. Chapman & Hall, New York.

Reeves, W. C., J. L. Hardy, W. K. Reisen, and M. M. Milby. 1994. Potential effect of global warming on mosquito-borne arboviruses. J. Med. Entomol. 31: 323–332.

Richardson, J. S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology 72: 873–887.

Ricklefs, R. E. 1984. Ecology. Chiron Press, New York.

Rueda, L. M., K. J. Patel, R. C. Axtell, and R. E. Stinner. 1990. Temperature-dependent development and survival rates of *Culex quinquefasciatus* and *Aedes aegypti* (Diptera: Culicidae). J. Med. Entomol. 27: 892–898.

SAS Institute. 1989. SAS/STAT user's guide, version 6. SAS Institute, Cary, NC.

Schneider, S. H. 1993. Scenarios of global warming, pp. 9–23. *In* P. J. Kareiva, J. G. Kingsolver, R. Huey, [eds.], Biotic interactions and global change. Sinauer, Sunderland, MA.

Service, M. W. 1985. Population dynamics and mortalities of mosquito preadults, pp. 185–201. *In* L. P. Lounibos, J. R. Rey, and J. H. Frank [eds.], Ecology of mosquitoes: proceedings of a workshop. Florida Medical Entomology Laboratory, Vero Beach, FL.

Sota, T., and M. Mogi. 1992a. Survival time and resistance to desiccation of diapause and non-diapause eggs of tem-

perate *Aedes* (*Stegomyia*) mosquitoes. Entomol. Exp. Appl. 63: 155–161.

Sota, T., and M. Mogi. 1992b. Interspecific variation in desiccation survival time of *Aedes* (*Stegomyia*) mosquito eggs is correlated with habitat and egg size. Oecologia 90: 353–358.

Steinwascher, K. 1982. Relationship between pupal mass and adult survivorship and fecundity for *Aedes aegypti.* Environ. Entomol. 11: 150–153.

Sutherst, R. W., G. F. Maywald, and D. B. Skarrat. 1995. Predicting insect distributions in a changed climate, pp. 60–88. *In* R. Harrington and N. E. Stork [eds.], Insects in a changing environment: 17th Symposium of the Royal Entomological Society 7–10 September 1993. The Royal Entomological Society, London.

Toma, T., S. Sakamoto, and I. Miyagi. 1982. The seasonal abundance of *Aedes albopictus* in Okinawajima, the Ryukyu archipelago, Japan. Mosq. News 42: 179–183.

Vitousek, P. M. 1994. Beyond global warming: ecology and global change. Ecology 75: 1861–1876.

Washburn, J. A., and E. U. Hartmann. 1992. Could *Aedes albopictus* (Diptera: Culicidae) become established in California tree holes? J. Med. Entomol 29: 995–1005.

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