Dynamic Life Table Model for *Aedes aegypti* (Diptera: Culicidae): Analysis of the Literature and Model Development

D. A. FOCKS, D. C. HAILE, E. DANIELS, AND G. A. MOUNT

Medical and Veterinary Entomology Research Laboratory, USDA-ARS, Gainesville, FL 32604


**ABSTRACT** The container-inhabiting mosquito simulation model (CIMSIM) is a weather-driven, dynamic life table simulation model of *Aedes aegypti* (L.). It is designed to provide a framework for related models of similar mosquitoes which inhabit artificial and natural containers. CIMSIM is an attempt to provide a mechanistic, comprehensive, and dynamic accounting of the multitude of relationships known to play a role in the life history of these mosquitoes. Development rates of eggs, larvae, pupae, and the gonotrophic cycle are based on temperature using an exponential approach. Larval weight gain and food depletion are based on the differential equations of Gilpin & McClelland compensated for temperature. Survivals are a function of weather, habitat, and other factors. The heterogeneity of the larval habitat is depicted by modeling the immature cohorts within up to nine different containers, each of which represents an important type of mosquito-producing container in the field. The model provides estimates of the age-specific density of each life stage within a representative 1-ha area. CIMSIM is interactive and runs on IBM-compatible personal computers. The user specifies a region of the world of interest; the model responds with lists of countries and associated cities where historical data on weather, larval habitat, and human densities are available. Each location is tied to an environmental file containing a description of the significant mosquito-producing containers in the area and their characteristics. In addition to weather and environmental information, CIMSIM uses biological files that include species-specific values for each of the parameters used in the model. Within CIMSIM, it is possible to create new environmental and biological files or modify existing ones to allow simulations to be tailored to particular locations or to parameter sensitivity studies. The model also may be used to evaluate any number and combination of standard and novel control methods.

**KEY WORDS** *Aedes aegypti*, population dynamics, computer modeling

Dengue viruses currently are the most important arthropod-borne viruses transmitted to man, whether judged in terms of the number of human infections or the number of deaths (Rosen 1983). Artificial and natural containers are the immature habitat of mosquitoes involved in the transmission of these viruses. Familiar examples include *Aedes* (Stegomyia) *aegypti* (L.) (cosmopolitan within the 20° isotherms), *Aedes* (S.) *albopictus* (Skuse) (southern continental Asia, Southeast Asia, eastern North America, southern Brazil), *Aedes* (Gymnometopa) *mediovittatus* (Coquillett) (Caribbean Basin), *Aedes* (S.) *africana* (Theobald), and *Aedes* (S.) *leucocephalus* (Newstead) (tropical Africa), *Aedes* (Finlaya) *nico* (Ludlow) complex (Southeast Asia, southern continental Asia), and *Aedes* (S.) *polynesiensis* Marks (southern Pacific). In many instances, the population dynamics of the vector appear to be the key regulatory factors influencing the endemicity–epidemicity of dengue (Gould et al. 1970, Moore et al. 1978). Even in areas where other non-entomological factors are probably regulatory (Sheppard et al. 1969), suppression will continue to involve mosquito control until vaccines become available on a widespread basis. For these reasons, our goal of developing a dengue transmission model begins with a model of the population dynamics of the primary urban vector, *Ae. aegypti*.

Our article develops a life table-based simulation model of the population dynamics of *Ae. aegypti* and similar diapausing *Aedes* Meigen mosquitoes that inhabit artificial and natural containers. The model, the container-inhabiting mosquito simulation model (CIMSIM), was designed to provide entomological inputs to a second model, DENSIM, which simulates the dynamics of dengue (DEN) virus transmission among humans. The intent of these modeling efforts is to provide a comprehensive, interactive, and dynamic accounting of the current understanding of the multitude of relationships known or believed to play a role in the ecology of these viruses in human populations.
Several objectives have prompted this work. Foremost is the development of adequate models that are rigorous and testable; the value and subsequent use of CIMSIM and DENSIM will depend on their comprehensiveness and validation (Curry & Feldman 1987). A second goal is to identify areas where current knowledge about the systems is inadequate or lacking; this occurs during the developmental process and through subsequent parameter sensitivity studies. Once validated, an important role of the models will be the investigation of system behavior; e.g., the interactions among, and the relative importance of, factors such as temperature, virus virulence, vector competence, and human and mosquito density on transmission rates, the nature of the endemic–epidemic state, and the relationship between mosquito suppression, herd immunity, and transmission. We hope to use these models to predict the dynamics of epidemics and the receptivity of new areas to dengue virus. The models also will be used to evaluate, develop, and optimize various control strategies and to estimate parameters that are difficult, impossible, or expensive to measure in the field (Birley 1970). Finally, the models are designed to serve as teaching aids, allowing researchers and operational personnel to develop insight into the behavior of a very complicated, nonlinear dynamical system and how it may be modified to reduce mosquito-borne disease in a changing environment.

Overview of Model

CIMSIM is a deterministic, dynamic life table simulation model (Halle & Mount 1987, Focks et al. 1988, Mount et al. 1991) which produces mean-value estimates of various parameters for all cohorts of a single species of Aedes mosquito within a representative 1-ha area. CIMSIM is basically a cohort accounting program that maintains information on abundance, age, development with respect to temperature and size, weight, fecundity, and gonotrophic status. With few exceptions, the various processes are simulated mechanistically. The accounting is made dynamic by calculating, on a daily basis, the number of each cohort that will pass to the next age or stage as a function of a host of variables and relationships. For example, development times of eggs, larvae, pupae, and the duration of the gonotrophic cycle are based on temperature using an enzyme kinetics approach (Sharpe & DeMichele 1977). The basis of larval weight gain, food depletion, and fasting are based on the differential equations of Gilpin & McClelland (1979), modified to compensate for the influence of temperature. Fecundity is modeled as a function of pupal size, which in turn is a function of the recent history of larval abundance, food, and temperature. All survivals are tied to temperature, and for adults and eggs, the saturation deficit as well; larval survival is also a function of fasting and fat body reserves. Our modeling goals and the complexity of the systems involved have precluded a strictly mathematical approach such as that of Dye (1864).

The heterogeneity of the larval habitat is depicted by modeling the cohorts of eggs, larvae, and pupae within up to nine different container types, each of which represents an important mosquito-producing container in the field. For instance, in substantial areas of New Orleans, LA, the most common containers include tires, 1-gal (3.8-liter) buckets, and drink bottles (Focks et al. 1991); whereas in Bangkok, Thailand, the common containers include the ong jar, flower pot plates, and ant traps (Southwood et al. 1972). Adult production from these representative containers is combined, the output of each type being scaled to reflect its relative abundance. The model contains a database of container types from which the user may select and use with or without modification. It is also possible to describe entirely new containers. Containers are characterized by size, method of water loss and gain, location and abundance, and larval food.

Because microclimate is a key determinant of survival and development for all stages, CIMSIM also contains an extensive database of daily weather information for a number of cities around the world for the past 25–40 yr. Adult microclimate is assumed to be the same as the daily local weather. Forimmatures, however, CIMSIM calculates daily water temperatures and water gains and losses for each of the representative containers based on local weather, container characteristics, and location.

CIMSIM assumes that the underlying mechanisms responsible for the salient biological characteristics of different nondiapau sing container-inhabiting Aedes are substantially similar. A third database in CIMSIM contains biological profiles, one for each species where data and analysis have permitted development. Selecting an existing biological parameterizes CIMSIM for that species; it is possible from within the program to create new profiles or modify existing files.

The final database within CIMSIM contains location-specific information. Here the user can associate with a location name, the species of mosquito to model, a beginning year and weather dataset for the simulation run, the containers to be used to describe the location, and local vertebrate host abundance and availability. Again, it is possible to edit the information on each location and create new locations. In this manner, it is fairly straightforward to describe in some detail the local environment to be simulated.

CIMSIM runs on MS–DOS-compatible computers with a minimum video graphic capability
Table 1. Default containers and associated characteristics

<table>
<thead>
<tr>
<th>Name</th>
<th>Ht, cm</th>
<th>Length x width, cm</th>
<th>Covered?</th>
<th>Monthly rate of turnover</th>
<th>Sun exposure</th>
<th>Filling method</th>
<th>Watershed ratio *</th>
<th>Reduction in evaporative loss due to container cover</th>
<th>Draw-down amount, liters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ant trap</td>
<td>3</td>
<td>15</td>
<td>No</td>
<td>0.10</td>
<td>0</td>
<td>Manual</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bucket, 5 gal</td>
<td>36</td>
<td>30</td>
<td>No</td>
<td>0.10</td>
<td>0.25</td>
<td>Rain</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Bucket, 1 gal</td>
<td>45</td>
<td>17</td>
<td>No</td>
<td>0.10</td>
<td>0.25</td>
<td>Rain</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cistern</td>
<td>175</td>
<td>150 x 200</td>
<td>Yes</td>
<td>0.10</td>
<td>0.75</td>
<td>Rain</td>
<td>10</td>
<td>0.8</td>
<td>20</td>
</tr>
<tr>
<td>Drink bottle a</td>
<td>20</td>
<td>8</td>
<td>No</td>
<td>0.10</td>
<td>0.25</td>
<td>Rain</td>
<td>0.25</td>
<td>0.5</td>
<td>-</td>
</tr>
<tr>
<td>Drum, 55 gal</td>
<td>35</td>
<td>37</td>
<td>Yes</td>
<td>0.10</td>
<td>0</td>
<td>Manual</td>
<td>0</td>
<td>-</td>
<td>10</td>
</tr>
<tr>
<td>Leaf axil</td>
<td>5</td>
<td>4</td>
<td>No</td>
<td>0.10</td>
<td>0.25</td>
<td>Rain</td>
<td>3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Ong jar</td>
<td>50</td>
<td>30</td>
<td>Yes</td>
<td>0.10</td>
<td>0</td>
<td>Rain</td>
<td>10</td>
<td>0.9</td>
<td>10</td>
</tr>
<tr>
<td>Rock hole</td>
<td>20</td>
<td>35</td>
<td>No</td>
<td>0.10</td>
<td>1</td>
<td>Rain</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Tire b</td>
<td>20</td>
<td>18</td>
<td>No</td>
<td>0.10</td>
<td>0.25</td>
<td>Rain</td>
<td>0.6</td>
<td>0.3</td>
<td>-</td>
</tr>
<tr>
<td>Tree hole</td>
<td>15</td>
<td>10</td>
<td>No</td>
<td>0</td>
<td>0.25</td>
<td>Rain</td>
<td>3</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* If the value for Watershed ratio is 0, the container is manually filled.

a Note that while tires and drink bottles are not normally covered, their physical shapes reduce their ability to intercept rainfall and reduce evaporative losses; hence, the fractional values in columns labeled Watershed ratio and Reduction in evaporative loss due to container cover.

of VGA; a math coprocessor and 386 or later versions of the central processing unit (CPU) are strongly recommended. A simulation run of 1 yr would take >1 hr on a 286-based computer and >3 min on a 486 system with a clock speed of 33 MHz. The software was developed using the Microsoft Basic Professional Development System. The executable module of CIMSIM is ~412 kbytes in size; weather files currently occupy ~13 Mbytes of disk space. The program uses menus from which selections can be made and default values inspected or changed. In the following sections, a description is presented of how the various factors and relationships known to influence *Ae. aegypti* and other container-inhabiting mosquitoes are accounted for in CIMSIM. The particular parameter values presented reflect the biology of *Ae. aegypti*.

Environment

Meteorological Data. Daily meteorological data, primarily from government experiment stations, airports, and civilian weather stations, are used in CIMSIM. Required variables include maximum and minimum air temperature (°C), precipitation (mm), relative humidity (%), and saturation deficit (mbar). Equations and relationships used to provide simulation estimates of larval water temperatures, water gains and evaporative losses, and adult microclimate from the weather station data on atmospheric conditions are presented in following sections.

Immature Habitat. An accounting of the dynamics of the immatures within the representative area is accomplished by simulating up to nine of the most common (or most important) mosquito-producing containers in the area. As an aid to specifying the characteristics of these representative containers, the user is supplied with an online database of commonly found natural and artificial containers (Table 1); associated with each is a list of default values for the parameters used to characterize each container. A description of these parameters and their relationships to fluctuations in water temperature and depth follows.

Specification of Physical Parameters. The abundance of each of the representative containers is specified by the average number per ha.

We assume that this number reflects the equilibrium of arrival and loss rates and specifies a parameter (monthly turnover rate) to indicate what proportion of a population of containers is lost and replaced from one month to the next. This has ramifications only when simulating control efforts such as source reduction. Container shapes are assumed to be either rectangular or cylindrical, and physical size is specified as height by length by width or as height by diameter (cm). The exposure of a container to direct sun influences water temperatures; this parameter (SunExposure) ranges in value from zero for containers located indoors or in full shade to one for situations in full sun. The user may also specify whether the opening of a container has some sort of cover over it, and if it does, to what degree normal evaporative losses are reduced by it (range, zero to one). Although containers such as discarded drink bottles and tires normally are not covered, their shape does limit evaporative losses; this may be specified here. Another parameter (Watershed area) allows specification of the ratio of water depth increase within the container to the amount of rainfall. For most outdoor, rain-filled containers, this parameter has a value of one. The watershed area of cisterns and other containers filled via runoff from a roof could range from 10 to >100; for containers such as tires and narrow-mouth drink bottles, the ratio may be <1. The parameter Drawdown indicates a daily amount (liters) manually removed from
domestic water storage containers, such as a rain-
filled cistern.

Specification of Food. The final parameters
specified for each container concern the seasonal-
ality of daily arrival and loss rates of food. The
three inputs are (1) the initial amount of food
present in terms of milligrams of liver powder (or
the energy equivalent in other foods), (2) a daily
average amount (mg) of food added to or pho-
synthetically created within the container during
each month, and (3) the daily proportion of accu-
nulated food that decomposes or is otherwise
lost from the container. Losses from larval con-
sumption are discussed below. For purposes of
comparing CIMSIM with other published labo-
ratory studies, we assume yeast and liver powder
are equivalent food sources (Gilpin & McCle-

Calculation of Water Temperatures. Water
temperature is an important factor influencing
the development rate and survival of all imma-
ture stages. Although it is possible to have CIM-
SIM use external files of observed maximum and
minimum water temperatures, these data nor-
ma}ly are not available; therefore, it is necessary
to estimate temperatures within the representa-
tive containers. CIMSIM assumes that water
temperature fluctuations are influenced by air
temperature, solar insolation, and container size.
The following expressions for daily maximum
and minimum water temperature (°C) and evacu-
porative loss (equations 1–3) were developed (Reg
Procedure, SAS Institute 1988) from an unpub-
lished field study conducted in Gainesville, FL,
where these variables were monitored in 12 con-
tainers for 76 d and compared with data from an
adjacent weather station (observed temperatures
ranged from 11 to 42°C and 9 to 36°C in water
and air, respectively):

\[
WaterTemp_{\text{max}} = 15.03 + 0.27 \times AirTemp_{\text{min}} \\
+ 0.01 \times AirTemp^2_{\text{max}} + 7.69 \times SunExposure^2
\]  

(1)

\[
WaterTemp_{\text{min}} = 5.02 - 1.36 \times SunExposure \\
+ 0.81 \times AirTemp_{\text{min}} + 0.001 \times AirTemp^2_{\text{max}}
\]  

(2)

Because the existence of the occasional large
(or protected) container is often an important fac-
tor permitting the overwintering of Ae. aegypti
in temperate cities (the so-called "mother wall"
of Chandler [1945]), moving averages of the
daily values of both WaterTemp_{\text{max}} and Water-
Temp_{\text{min}} are used in the model for containers
with water volumes >5 liter. The rationale is to
simulate the attenuated temperature fluctuations
caused by thermal inertia in the larger contain-
ers. The length of the moving average is deter-
mined by the water capacity of the container: for
volumes >500 liter, a 4-d moving average is
used; for 100–500 liter, 3 d; for 5–100 liter, 2 d;
and for <5 liter, simply the daily values are used.
WaterTemp_{\text{max}} and WaterTemp_{\text{min}} (or their
associated moving averages if the volume is >5 liter)
are used in calculating survivals as a function of
temperature extremes; a mean of the maximum
and minimum is used in thermal development cal-
culations (\(T_d\)) (equation 4).

Calculation of Water Gains and Losses. Daily
evaporative loss (cm) from an uncovered con-
tainer is given by the following equation:

\[
\text{Evaporative Loss} = 0.93 + 0.28 \times SunExposure \\
- 0.01 \times \% \text{Relative Humidity}
\]  

(3)

The amount of evaporative loss in covered con-
tainers would be reduced by the amount specified
by the user as indicated above. If a manual
drawdown was specified, total loss reflects both
evaporative loss and drawdown. Daily water
gains in rain-filled containers are simply the
product of rainfall and the watershed ratio for
that container. For manually-filled containers,
we assume that gains and losses are equivalent
and that water levels fluctuate daily. Water is
replenished daily from a village water source such
as a standpipe or faucet.

Vertebrate Hosts. Although the availability of
bloodmeal hosts rarely is considered limiting in
the population dynamics of Ae. aegypti, a routine
described below has been included in CIMSIM to
allow specifying a relationship between adult
survival and the ratio of the numbers of blood-
seeking females and hosts. In terms of charac-
terizing the environment, the model is asked to sup-
ply estimates of the numbers of humans and
other vertebrates (Macdonald 1967) within the
representative area and their respective avail-
abilities during the biting activity period of
the mosquito.

Biological Relationships

Temperature-Dependent Development. Com-
puter simulation is being increasingly used to
study the dynamics of biological systems. This
has been accompanied by an interest in mathemat-
ical models to describe poikilotherm growth and
development as a function of temperature.
The day-degree or temperature summation rule
is used widely in entomological studies because
it is easy to use and (within certain temperature
limits) approximates observed rates. Because the
day-degree method assumes development rates
to be proportional to temperature, day-degree
projections are valid only for the linear portion
of the S-shaped curve of development (for example,
see Fig. 5 in the region between 20 and 27°C).

\[
\text{Enzyme Kinetics Model.} \text{ CIMSIM uses a}
\]  

model derived by Sharpe & DeMichele (1977)

Based on absolute reaction rate kinetics of en-
zymes.
Table 2. Coefficients for the enzyme kinetics model of Sharpe & DeMichelis (1977) relating development rates to temperature

<table>
<thead>
<tr>
<th>Stage or process</th>
<th>( P_{25^\circ C} )</th>
<th>( \Delta H^*_{A} )</th>
<th>( \Delta H^*_{H} )</th>
<th>( T_{1/2H} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Embryogenesis</td>
<td>0.01066</td>
<td>10,758.13</td>
<td>100,000.00</td>
<td>14,184.50</td>
</tr>
<tr>
<td>Larval development</td>
<td>0.00873</td>
<td>25,018.51</td>
<td>55,990.75</td>
<td>304.58</td>
</tr>
<tr>
<td>Pupal development</td>
<td>0.01610</td>
<td>14,931.94</td>
<td>-472,379.00</td>
<td>148.45</td>
</tr>
<tr>
<td>Gonotrophic cycle</td>
<td>0.00988</td>
<td>15,725.23</td>
<td>1,756,481.07</td>
<td>447.17</td>
</tr>
</tbody>
</table>

zymes for the temperature-dependent developmental rates of eggs, larvae, pupae, and the duration of the gonotrophic cycle. This model assumes that, other factors not limiting, the rate of development is determined by a single rate-controlling enzyme which is denatured reversibly at high and low temperatures. The form of the model used here (equation 4) is a version simplified by Schoolfield et al. (1981) to allow parameter estimation from observed data using nonlinear regression (NLLIN procedure, SAS Institute 1988) using Marquardt's (1963) searching algorithm; it assumes high-temperature inactivation. Parameterization is an iterative process—initial parameter estimates for \( P_{25^\circ C} \) (0.006 h\(^{-1}\)) and \( T_{1/2H} \) (313.9 K) were taken from McHugh & Olson (1982); initial estimates for \( \Delta H^*_{A} \) and \( \Delta H^*_{H} \) were set arbitrarily at 10,000 and 100,000 cal mol\(^{-1}\), respectively (Schoolfield et al. 1981).

\[
r(T) = \frac{P_{25^\circ C}(T/298) \exp[(\Delta H^*_{A}/R)((T/298) - (1/T))]}{1 + \exp[(\Delta H^*_{H}/R)((1/T_{1/2H}) - (1/T))]} - \sum_{t=0}^{n} r(T_t) \tag{4}
\]

\[
CD_t = \sum_{t=0}^{n} r(T_t) \tag{5}
\]

In these expressions, \( r(T) \) represents the development rate (h\(^{-1}\)) at temperature \( T \) (K) on day \( t \); \( T \) is the moving of the mean average (K) of WaterTemp\(_{max} \) and WaterTemp\(_{min} \) (equations 1 and 2); AirTemp\(_{max} \) and AirTemp\(_{min} \) are used in the case of gonotrophic development; \( \mu_{25^\circ C} \) is the development rate (h\(^{-1}\)) at 25°C assuming no temperature inactivation of the critical enzyme, \( \Delta H^*_{A} \) is the enthalpy of activation of the reaction that is catalyzed by the enzyme (cal mol\(^{-1}\)), \( T_{1/2H} \) is the temperature (K) where 50% of the enzyme is inactivated (cal mol\(^{-1}\)), and \( T \) is the universal gas constant (1.987 cal mol\(^{-1}\) deg\(^{-1}\)), and \( CD \) represents cumulative development.

Parameter estimates (Table 2) were developed for equation 4 from data found in the literature and cited in the sections below on development rates versus temperature. Each day, for the gonotrophic cycle and each life stage in each of the representative containers, the appropriate mean temperature is used in a form of equation 4 which has been fitted with the parameters for the particular life stage, and \( r(T) \) is calculated. Development from a thermal point of view accumulates (\( CD \)) and is considered to have been completed on the day when \( CD > 0.95 \) (equation 5); in a discrete model with a daily time step, setting the completion sum to be slightly \(< 1 \) results in the average time being closer to 1.00. In CIMSim, the duration of embryonation, the pupal stage, and gonotrophic cycles are determined solely on the basis of temperature. Larval development is tied to temperature in a similar fashion (minimum thermal requirement), but the additional complications of the influence of temperature on rates of food finding, assimilation, and metabolism and the interaction of minimum pupation weight thresholds and larval age also is taken into account.

Calculation of Daily Survival Rates. In CIMSim, we assume an exponential model of survival for all stages; i.e., mortality rates are independent of age. The type of underlying model assumed for adult survival in CIMSim may be especially significant later in DENSIM in the context of vectoria capacity. Recently it has been shown for many species of tropical mosquitoes that an exponential model is inaccurate and that the Gompertz model, in which survival is proportional to (the logarithm of) age, is more appropriate (Clements & Paterson 1981). This work, however, noted that Aedes aegypti was an exception, with daily survival rates being independent of the age of the female. Computationally, daily rates are the product of a nominal daily survival and a series of one or more survival factors. The nominal daily survival term reflects mortality and mortality caused by natural hazards in the environment not otherwise taken into account by specific factors. We do not see nominal survival rates commonly or significantly operating as functions of density (Southwood et al. 1972, Gilpin & McClelland 1978, Subra & Mouchet 1984). Survival factors, on the other hand, reflect the additional stress of temperature extremes, dryness, and temperature changes, and, in the case of larvae and adults, some density-dependent factors; their values can range from 1, when conditions are not adverse, to 0.

Developing realistic estimates for temperature-related daily survival is problematic because, typically, the literature reports survival only as a function of constant temperatures for various nonstandard exposure times. An additional complication is that we know only the maximum (or minimum) temperature; the actual temperature profile is unknown.
Eggs (Fig. 1). There is very little field or laboratory data on which to base our estimates of egg development or survival. The values given below are used as defaults in the Ae. aegypti biology profile; they can be changed as desired. There is no indication in the literature that egg
crowding influences egg survival nor subsequent oviposition, and CIMSIM, therefore, assumes no interference-type density-dependent population regulating mechanisms operating on this stage.

Embryonation. Very little specific information has been published on the rate of embryonation as a function of temperature in *Ae. aegypti*. Our analysis was based on data points taken from Atkin & Bacot (1917), Johnson (1937), Gander (1951), and Horsfall (1955). Nonetheless, the parameter estimates developed (Table 2) with these data for equation 4 result in predicted development times which agree well with specific and anecdotal reports such as those of Horsfall (1955): “—incubation is completed within 4 days at summer temperatures.” Fig. 2 presents observed and predicted development rates versus temperature. As additional visual and statistical indicators of the adequacy of the parameterized equation, a linear regression is included in the figure of the predicted values plotted against their corresponding observed values; the coefficient of determination ($R^2$), the intercept ($\alpha_0$), slope ($\alpha_1$), and 95% CIs (CI$_{95\%}$) of $\alpha_0$ and $\alpha_1$ of the regression (Proc REG, SAS Institute 1988) are reported in the legend (Focks et al. 1999).

Survival. *Aedes aegypti* eggs die in exponential fashion in the laboratory as a function of temperature and humidity but do so independently of egg density (Gilpin & McClelland 1979). In CIMSIM, we assume nominal daily egg survival to be 0.99 based on field observations in peridomestic artificial and natural containers in shaded habitats (Trpis 1972) where predation was excluded.

The survival factor for temperature extremes (Fig. 3) was developed from many laboratory sources (Reed et al. 1901, Marchoux et al. 1903, Bacot 1916, Macle 1920, Bliss & Gill 1933, Christophers 1960). The value for the survival factor reflecting egg desiccation (Fig. 4) is set to 1.00 for all water-holding containers irrespective of humidity; we assume moisture is not limiting in such situations. In dry containers, if SunExposure $>0.85$, the factor is set to 0.95 based upon observed survivals in sun-exposed coral rock holes during the dry season on the Tanzanian coast (Trpis 1972). This ad hoc solution reflects the fact that weather station data on atmospheric moisture does not reflect the harsh environment within such containers. For dry containers with SunExposure $\leq 0.85$, the survival factor varies with the saturation deficit, a parameter reflecting both atmospheric moisture and temperature (Fig. 4) (Fielding 1919, Buxton & Hopkins 1927, Christophers 1960). Because oviposition occurs within several cm of the water line, we assume for all container types that eggs remain moist for the first few days when they are especially susceptible to desiccation (MacGregor 1916).

Predation by ants and cockroaches is a common source of *Ae. aegypti* egg loss in the laboratory (personal observation), and egg predation by ants in the field has been reported (Buxton & Hopkins 1927). Summerlin & Welch (1984) and
Dunn (1926) observed ants in >85% of all water-holding rot cavities in trees in Texas and Nigeria, respectively. Focks et al. (1982) reported that ≈40% of all Aedes aegypti exuviae were removed from the water surface by foraging ants in small plastic containers located outdoors in New Orleans, LA. Sachett (1988) reported observing in New Orleans, LA cockroaches, ants, and pillbugs eating Aedes aegypti and Aedes albopictus eggs in the field. Because foraging is presumably temperature-related, the biology file allows for specifying the rate as a function of temperature. This factor is set provisionally to 1.0 at or below 20°C (after Brenner & Pierce [1991] and Porter & Tschinkel [1987]) and to 0.7 at or above 30°C; between 20 and 30°C, it varies linearly between 1.0 and 0.7. This treatment is inadequate; however, there are no data on rates of ant predation in the field, and it is likely that rates in tropical and temperate regions would be significantly different, even at identical temperatures.

Hatch. The minimum temperature permitting hatch is set at 22°C (Marchoux et al. 1903). This may be too high for temperate strains of Aedes aegypti, because Christopher (1960) reports minimums between 13 and 20°C. CIMSMA assumes that 19.7% of all newly embryonated eggs hatch spontaneously without flooding and that 90.3% of the remaining eggs hatch each day of submergence; eggs that are submerged on the day when embryonation is completed hatch immediately (Bacot 1916, Southwood et al. 1973).

Larvae (Fig. 1). Previous studies have concluded that Aedes aegypti populations are regulated primarily by intraspecific competition in the larval stage and that the nature of this density-dependent mechanism is competitive exploitation of food resources (Southwood et al. 1972, McDonald et al. 1977, Focks et al. 1978, Gilpin & McClelland 1979, Dye 1984b). There is less of a consensus on the significance of interference competition—chemical or physical. Laboratory studies are equivocal and very likely misleading because extremely high larval densities were used; i.e., typically hundreds to several thousand larvae per liter (e.g., Moore & Fisher 1969, Dye 1982) versus typical field densities of only a few larvae per liter (Southwood et al. 1972, Focks et al. 1981). Therefore, in the development of CIMSMA, we have followed Bar-Zeev (1937), Gilpin & McClelland (1979), and Dye (1984b) in dismissing any kind of significant interference.

Development as a Function of Food, Larval Size and Density, and Temperature. Data for estimating the parameters of equation 4 for larval development as a function of temperature under conditions of nonlimiting food were taken from Gilpin & McClelland (1979); averages of the male and female rates were used (Fig. 5). Pupation follows the completion of a minimum thermal experience as described above (equations 4 and 5) and achieving a minimum larval weight.

![Fig. 5. Developmental rate per hour of Aedes aegypti larvae to median pupation (data from Fig. 1 in Gilpin & McClelland 1979) as a function of temperature. Prediction based on enzyme kinetics model of Sharpe & DeMichele (1972) using parameter estimates in Table 2. Insert: linear regression of observed and predicted development times. R² = 99.6%; a₀ = -2.5, C⁰ = -11.9-8.6; c₂ = 1.6, Cg = 1.0-1.1.](image)

The rates of larval weight change, food exploitation and assimilation, and metabolism are believed to be governed by the following equations (equations 6 and 7) of Gilpin & McClelland (1979), which have been modified to reflect the influence of temperature:

\[
dW(t)/dt = a f(T imposed) \ [W(t) \ - \ \exp(-c \ F(t))] \tag{7}
\]

where \( t \) is time, \( W(t) \) is the dry weight (mg) of a larva or the average dry weight of individual larvae in a cohort at time \( t \), \( F(t) \) is the weight of food within the container in terms of milligram liver powder equivalents, and \( n(t) \) is the number of larvae in a cohort. Consumed food is assumed to be assimilated into larval biomass at a constant rate of \( 30\% \) (Gilpin & McClelland 1979). The rate of food exploitation increases as a power of body weight \( (W(t)^b; b = 0.8) \); i.e., large larvae can find and process food at a faster rate than small larvae. Food exploitation is also seen to vary with the density of food as a Type II functional response (Holling 1965). The \( 1 - \exp(-cF(t)) \) term results in the exploitation rate being proportional to food density when food density is low; with higher densities, however, the rate becomes increasingly independent of food abundance, simulating a saturation of the need or ability to process food. The constant \( c = 0.1 \) determines the rate of approach to the asymptote at saturation. The \( a_f \) term specifies the metabolic requirements of the larva and equals the rate of weight loss when food is de-
pleted \( (d_1 = 0.016, d_2 = 0.667) \); in contrast to weight gains of a few hundred percent per day when food is in excess, fasting weight losses are on the order of only a few percent per day.

The final element, \( f(T_f) \), provides a chronological basis as a function of temperature \( T_f \). The original experiments used to parameterize the chronological equations were conducted at a fixed temperature of 26°C, and \( f(T_f) \) was replaced with a constant term, \( f_r = 0.001 \) to put the otherwise physiological equations onto a chronological basis at that single temperature. Our temperature function has the following form:

\[
f(T_f) = f_r \frac{r(T_f) - r(13.4°C)}{r(26°C) - r(13.4°C)}
\]

The second term in the numerator serves to set \( f(T_f) \) to zero when \( T_f \) is at the lower developmental threshold of 13.4°C (Bar-Zeev 1955); this was necessary because the kinetics model (equation 4) inappropriately predicts a rate at this temperature of 0.010 hr⁻¹ or 29.5 d (see Fig. 5). The value of \( f(T_f) \) is \( f_r = 0.001 \) at 26°C.

Survival. Larval survival as a function of temperature is presented in Fig. 3; these default values reflect reports cited in Horsfall (1955) and the observations of Bar-Zeev (1958) and Rueda et al. (1990). A second survival factor reflecting desiccation is set to 0.05 if the container dries out. Gilpin & McClelland (1979) report that genetic deficiencies cause some larval death (=3% in Ae. aegypti) irrespective of environmental circumstances. Although this loss occurs over the course of larval development, it is applied when pupation occurs to simplify computations.

The final larval survival factor reflects mortality associated with fasting. We posit the existence of a reserve lipid state used when metabolic losses exceed food inputs (Weidling 1928, Wigglesworth 1944, Chambers & Klowden 1990). Equation 9 gives an empirical relationship between body weight, \( W(t) \), and the proportion of lipid, \( L(t) \), for Ae. aegypti larvae that have always experienced a positive weight gain (Gilpin & McClelland 1979). Equation 10 indicates the amount of \( L(t) \) available as reserves—\( R(t); L_{min} (= 0.15) \) is the proportion of lipids involved in structural components such as membranes and is considered unavailable to fasting.

\[
L(t) = 0.059 \log(W(t) + 6.9)
\]

\[
R(t) = L(t) - L_{min}
\]

Based on Fig. 14 in Gilpin & McClelland (1979), the factor reflecting fasting survival in a simulation model is set to 1.00 provided \( dW/dt \geq 0 \). When fasting occurs and lipid reserves are available (i.e., \( R(t) \geq 0 \)), the fasting factor is set to 0.95; otherwise, if the reserves are depleted, the factor is set to 0.50. Weight gains following fasting are considered to exclusively replenish reserves until the prefasting weight gain is regained and equation 9 is again applicable. Larvae are killed if \( W(t) \) goes below 0.003 mg or if \( CD_t > 8.0 \).

**Numeric Calculations.** The following three calculations are made daily for each representative container. (1) The amount of food present is calculated. Gilpin & McClelland (1979) report and provide a theoretical basis for the fact that variation in food addition is important to population success. To simulate the stochastic arrival of food, we add food every third day. The contribution of cadavers, a second source of food, considered to be 40% as effective as a live larva (Gilpin & McClelland 1979), is added the day following death. Finally, food loss from decay is calculated. (2) A set of equations 6 and 7 for each cohort within the container is simultaneously solved using Euler’s method (Press et al. 1986) with a step size of 1/6 day. (3) The various survival factors are applied reflecting conditions within the particular container.

Fig. 6 presents a comparison of observed and CIMSIm-predicted larval dry weight gain trajectories for larval development in a rearing system involving a single 40-μg pulse of food into cups containing 8, 51, or 128 newly hatched Ae. aegypti (Fig. 11 in Gilpin & McClelland 1979). For all larval densities, food was in excess for the first 2 d; thereafter, food depletion progressively retarded growth, especially in the cups with high larval densities. The fits depicted in Fig. 6 reflect the adequacy of Gilpin & McClelland’s equations rather than an independent validation of CIMSIm; they are presented primarily as a verification that their equations have been implemented accurately in the model. Similarly, Fig. 7 presents a comparison of fasting survivorship curves.
Nominal data show a relationship to temperature, with lower pupation temperatures occurring at temperatures below 25°C. This loss of viability is temperature-dependent, and the higher pupation temperatures observed at 34°C and 36°C, leading to a loss of 100% and 75%, respectively. This pattern is consistent with the data presented in Figure 7, which shows a decrease in pupation success as temperature increases.

Emergence was assessed at different temperatures and sex ratios. The data from Figure 8 suggest that emergence is significantly affected by temperature, with lower emergence rates observed at higher temperatures. This is particularly evident at the 34°C and 36°C temperatures, where emergence rates are reduced to 50% and 25%, respectively.

Adults. Adult emergence was monitored through each of the temperature treatments, with data showing significant differences in emergence rates. The data from Figure 8 confirm this trend, with lower emergence rates observed at higher temperatures. This suggests a temperature-dependent effect on adult emergence, with temperature affecting the rate and duration of maturation.

Gonotrophic cycle. The gonotrophic cycle in Aedes aegypti is affected by temperature, with data from Macdonald et al. (1971) showing a decrease in the length of the cycle as temperature increases. This is consistent with the data from Figure 8, which shows a decrease in the length of the cycle as temperature increases.

Pupation (Fig. 1). Survival and Development as a Function of Temperature. The Sharpe-DeMichie coefficients determined by Rueda et al. (1990) for the pupal development of Aedes aegypti were used to parameterize equation 4; their reported goodness-of-fit was $R^2 = 98%$. We assume that the rate of development in the pupa is a function only of temperature rather than previous larval nutrition or density (Wada 1965).
Nominal daily pupal survival and the relationship to temperature extremes (Fig. 3) are considered identical with those of larvae presented previously (see above for references), except that the loss of water within a container does not lower pupal survival as in the case of larvae.

Emergence and Sex ratio. Emergence occurs when $CD > 0.95$ (equations 4 and 5). We assume a loss of 17% during the process of eclosion (Southwood et al. 1972). Although extremely stressed (starvation) larval conditions favor the increased production of males (Brust 1968), we assume sex ratio to be independent of larval rearing conditions and that a constant 50.0% of the adults emerging are females (Southwood et al. 1972).

Adults. Adult Female Size. From the egg stage through eclosion, CIMSIM uses values for life history parameters that are averages for both sexes. Following emergence, however, CIMSIM accounts only for females, because female size is known or suspected of influencing fecundity, survival, and blood-feeding success and frequency (MacDonald 1956; Steinwascher 1982; Nasr 1986, 1991). The dry weights used in larval calculations are multiplied by 1.655 to convert to wet adult female weight (based on Table 5 in Rueda et al. 1990). A weighted and moving average of female weights of emerging cohorts from each of the representative containers is used as the nominal weight of females within the 1-ha environment.

Gonotrophic Cycle and Biting. Parameter values for the temperature-dependent rate of gonotrophic development (equation 4, Table 2) in Ae. aegypti were based on observations by MacDonald (1956), McClelland & Conway (1971), Pant & Yasuno (1973), and Nayar (1981). Some of the error in predicting gonotrophic development as a function of temperature (Fig. 9) stems from inconsistencies in the reported observations. The first cycle (Fig. 1), from emergence to oviposition, is considered to be completed on the day when $CD > 1.00$ (equation 5). Subsequent cycles, oviposition to oviposition, are somewhat shorter (completed on the day when $CD$ has increased by an additional 0.58), because the primary follicles are at stage II following oviposition rather than at stage I as in the case of newly emerged females (MacDonald 1956).

The biting rate will be an important consideration in DENSIM. In addition to being an obvious factor in the epidemiology of Ae. aegypti-borne disease, in some situations (see below) this parameter may be involved in density-dependent feedback on other life history parameters (e.g., McLaughlin & Focks 1990). We assume that larval rearing conditions influence not only adult size but energy reserves as well, so the frequency of taking more than one replete blood meal per gonotrophic cycle varies as a function of adult size (Fig. 10) (Hecht 1933, MacDonald 1956). Females from well-fed larvae emerge with lipid reserves adequate to develop ovaries to stage II, with the result that the first blood meal is sufficient to complete oogenesis. Currently, replete meals are sought on the second day of the first cycle and on the first day of subsequent cycles; any second replete feed within a cycle (Fig. 10) is considered to occur on the day following the first feed within that cycle (McClelland & Conway 1971). The total number of contacts between blood-seeking females and hosts per day within the 1-ha representative area is a product of the number of females seeking a replete feed and the average number of interrupted feeding attempts per replete feed; this parameter is currently set to 3 in the Ae. aegypti biology file.

Fecundity, Oviposition, and Survival. Fecundity is modeled as a function of wet female
weight (equation 12) based on the observations of Bar-Zeev (1957) and Nayar & Sauerman (1975). Nominal adult survival (0.91 d⁻¹) is modified by survival factors reflecting

\[
R_{\text{fecundity}} = 48.5 \text{ W}_{\text{female}}
\]

air temperature and moisture extremes (Fig. 4) based on reports listed in Horsfall (1953), Christophers (1960), and Fay (1964). Oviposition (Fig. 11) is programmed to occur within 0–4 cm of the water line (Christophers 1960), and females retain their eggs if average temperatures are below 22°C (Hoffmann 1971). It is likely, other things being equal, that small containers receive proportionately less oviposition than larger containers (Sartees 1960, 1967; Southwood et al. 1972). To approximate this, CIMSIM apportions the daily oviposition among the water-filled representative container types as a function of the product of density and size of each type (\(\ln(\text{volume} + 1)\) in liters).

It is possible in CIMSIM also to modify adult survival as a function of the ratio of the number of blood-seeking females and available hosts (Fig. 11). The number of hosts is the sum of the number of human and other vertebrate hosts times their respective availabilities during the period of biting activity of the mosquito; these factors are set in the location and biology files, respectively. This does not indicate that the availability of blood meals commonly limits the gonotrophic cycle of Ae. aegypti in the field. The ability to reduce female survival as a function of the ratio of bits to hosts is simply an \textit{ad hoc} method to investigate the effect of changing human behavior in response to high mosquito densities; i.e., the use of household sprays, mosquito coils, etc. Without data to do otherwise, this survival factor has been set to 1.0 for all levels of this ratio.

**Discussion**

There is a wealth of information on the biology of Ae. aegypti which has allowed us to develop an essentially mechanistic model which captures many of the important biological attributes of this species. This article describes the development of CIMSIM based on the biology of Ae. aegypti. A companion paper (Focks et al. 1983) provides a comprehensive laboratory and field validation of the model using data from several locations in the world; a third paper will discuss the population dynamics of Ae. aegypti and other species in temperate and tropical environments and will evaluate several integrated control strategies.

**Shortcomings of the Model.** In conclusion, we mention briefly some areas where CIMSIM probably requires improvement.

- **Microclimate for adults is assumed to be identical with weather station observations.** We know that adults seek out a microclimate, typically indoors, which probably does not correlate well with this type of data. This shortcoming may be critical regarding dengue transmission, given the role of temperature in the length of the extrinsic incubation period of virus (Watts et al. 1987).
- **Prediction of water temperature and evaporation is important, yet currently, our hydrological calculations are based only on a few months of data in a single temperate region.**
- **CIMSIM does not attempt to model the proportions of containers infected, only container productivity.** This is more of a problem in temperate regions than in tropical locations where seasonal fluctuations are minimal and most containers are not filled with rain; e.g., Bangkok, Thailand (Tonn et al. 1969).
- **The quality and quantity of data concerning the various facets of the biology of Ae. aegypti and its environment ranges widely.** This is reflected in the degree of rigor and accuracy with which we have modelled various subcomponents. The most obvious example is the precision with which larval development is handled on one hand and food inputs on the other—a completely unknown entity in the field. Given the fidelity in CIMSIM output to laboratory data where food inputs are known (Figs. 6 and 7; and Figs. 1 & 2 in Focks et al. 1983), we are comfortable fitting food levels to produced observed densities of larva and pupae.
- **We have not yet incorporated the changes to Gilpin & McClelland’s (1979) equations suggested by Dye (1982), making the variables \(a\) and \(c\) functions of age.** For the sake of simplicity, we have also ignored Birley’s (1979) consideration of the variable development period.

**Acknowledgments**

We acknowledge Robin S. Steele of our laboratory for the initial phases of programming CIMSIM and for the creation of numerous weather files. We also thank Debra L. Runyon and Hilda J. Snelling (USAF Envi...
References Cited

Alden, E. E. & A. W. Bacon. 1917. The relation between the hatching of the eggs and the development of the larvae of Stegomyia fasciata (Aedes calopus) and the presence of bacteria and yeasts. Parasitology 9: 452-536.


Received for publication 5 October 1992; accepted 11 June 1993.