

# Modeling the Population Dynamics of *Culex quinquefasciatus* (Diptera: Culicidae), along an Elevational Gradient in Hawaii

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**ABSTRACT** We present a population model to understand the effects of temperature and rainfall on the population dynamics of the southern house mosquito, *Culex quinquefasciatus* Say, along an elevational gradient in Hawaii. We use a novel approach to model the effects of temperature on population growth by dynamically incorporating developmental rate into the transition matrix, by using physiological ages of immatures instead of chronological age or stages. We also model the effects of rainfall on survival of immatures as the cumulative number of days below a certain rain threshold. Finally, we incorporate density dependence into the model as competition between immatures within breeding sites. Our model predicts the upper altitudinal distributions of *Cx. quinquefasciatus* on the Big Island of Hawaii for self-sustaining mosquito and migrating summer sink populations at 1,475 and 1,715 m above sea level, respectively. Our model predicts that mosquitoes at lower elevations can grow under a broader range of rainfall parameters than middle and high elevation populations. Density dependence in conjunction with the seasonal forcing imposed by temperature and rain creates cycles in the dynamics of the population that peak in the summer and early fall. The model provides a reasonable fit to the available data on mosquito abundance for the east side of Mauna Loa, Hawaii. The predictions of our model indicate the importance of abiotic conditions on mosquito dynamics and have important implications for the management of diseases transmitted by *Cx. quinquefasciatus* in Hawaii and elsewhere.

**KEY WORDS** Hawaii, *Culex quinquefasciatus*, population model, temperature, rainfall

SOUTHERN HOUSE MOSQUITO, *Culex quinquefasciatus* Say, a widely dispersed domestic mosquito, is a vector for several diseases that affect wildlife and humans. *Cx. quinquefasciatus* has been shown to transmit dog heartworm, *Dirofilaria immitis*; avian malaria, *Plasmodium relictum*; avian pox, *Poxvirus avium*; and West Nile virus (WNV) (Gubler 1966; Warner 1968; van Riper et al. 1986, 2002). *Cx. quinquefasciatus* was introduced to the Hawaiian Islands at the turn of the 19th century, probably as early as the 1820s (Hardy 1960). With the subsequent introduction of pox and then avian malaria, presumably from infected exotic birds and chickens (Henshaw 1902, van Riper et al. 1986, Tripathy et al. 2000), *Cx. quinquefasciatus* mosquitoes spread these diseases among native Hawaiian birds. In particular, avian malaria and pox have been implicated in the extinction of endemic Hawaiian avifauna (Warner 1968) and were demonstrated to have a large negative impact on remaining native bird populations in Hawaii, restricting the distribution of some species to higher elevations where mosquitoes are

absent (van Riper et al. 1986, 2002; Atkinson et al. 1996).

Despite its significance as a disease vector in Hawaii, relatively little is known about the ecology of *Cx. quinquefasciatus* in the Hawaiian islands. A recent extensive study on the Island of Hawaii (LaPointe 2000) has shown that these mosquitoes are present throughout the island, from sea level to ≈1,500 m in elevation. However, their population dynamics seems to change with elevation. At lower elevations, *Cx. quinquefasciatus* populations occur in high numbers with relatively little seasonal variation, although higher numbers are found during the third quarter of the year. In contrast, at middle (≈600–1000 m) and high (≈1,300–1,500 m) elevations mosquito numbers are much lower, and seasonality is more pronounced with large spikes once or twice a year (LaPointe 2000). These complexities in the population dynamics of *Cx. quinquefasciatus* can have important consequences for the transmission of malaria and pox and their interaction with potential avian hosts across the landscape.

Population dynamics of *Cx. quinquefasciatus* in Hawaii are influenced by several abiotic and biotic factors. First, mosquitoes are poikilotherms and therefore highly dependent on ambient temperature for successful development. Several studies have shown that

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immature stages of *Cx. quinquefasciatus* and other mosquito species exhibit a linear rate of development as a function of temperature, at least within the range of mean temperatures encountered in Hawaii (12–24°C) (Rueda et al. 1990, Oda et al. 1999, Alto and Juliano 2001b). Second, because *Cx. quinquefasciatus* is predominantly a cavity breeder in Hawaii, rainfall dynamics and cavity availability also influence population growth. Both desiccation and excessive rainfall events can influence adult and immature mosquito survival (Bradshaw and Holzapfel 1988, Mogi et al. 1996, LaPointe 2000, Alto and Juliano 2001a). Finally, within-cavity density-dependent effects can increase mortality of larvae and pupae in the species (Teng and Apperson 2000).

In this article, we propose a model that describes the population dynamics of *Cx. quinquefasciatus* along an elevational gradient on the Island of Hawaii. This model is one component of a larger modeling effort to understand the dynamics of malaria and pox in native forest birds along the eastern flank of Mauna Loa, Island of Hawaii. The model incorporates temperature and rainfall dependence and within-cavity density-dependent competition to generate population trajectories through time and at different elevations. **Demographic and temperature-dependent model parameters were based on field and laboratory data for *Cx. quinquefasciatus* collected from the literature.** Rainfall-dependent survival functions were calibrated to reflect the most realistic biological situations encountered by *Cx. quinquefasciatus* in the field. We explored parameter space of the most ecologically relevant parameters to determine their influence on model behavior. Our goal is to calibrate a sound biological model that can be used to simulate mosquito temporal patterns across the entire island and other sites where *Cx. quinquefasciatus* is present.

## Materials and Methods

**Structure of the Model.** We used a discrete-time population model to simulate the temporal dynamics of the mosquito population. Because the development rate of immature mosquitoes is dependent on ambient temperature, we used physiological ages based on degree-days required to achieve development, as opposed to chronological age or discrete immature stages. The model is of the general form

$$\mathbf{N}_{t+1} = \mathbf{A}(T, R, n) \mathbf{N}_t \quad [1]$$

where  $t$  is time measured in days,  $\mathbf{N}$  is a vector with the number of individuals in each physiological age, and  $\mathbf{A}$  is a transition matrix that is a nonlinear function of daily temperature ( $T$ ), daily rainfall ( $R$ ), and density dependence based on the number of immatures ( $n$ ). The general structure of the transition matrix is shown in Fig. 1. Table 1 lists abbreviations, variables, and parameters for the model. Explanation of each of the components is given in the sections below.

**Temperature Dependence.** The dependence of developmental rate on ambient temperature in mosquitoes introduces complications for the construction of

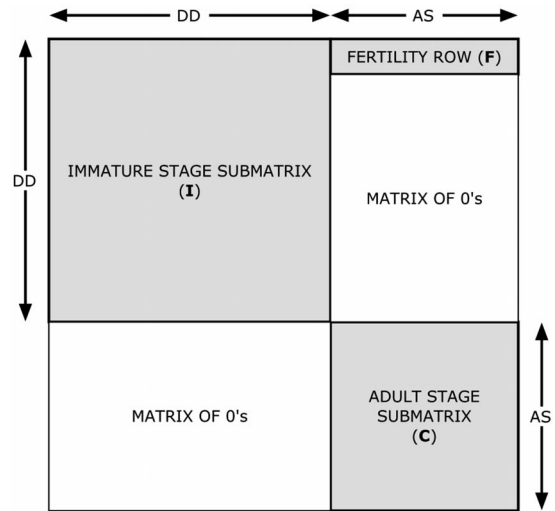


Fig. 1. General structure of the transition matrix  $\mathbf{A}$ . The upper left submatrix is the temperature-dependent component of the model. The structure of each submatrix is explained in detail in the text.

population models (Rueda et al. 1990). Normally, the transition probabilities describing development (e.g., probability of an instar 1 larvae becoming an instar 2 larvae) are constant. However, if developmental rates are temperature-dependent this constant-rate assumption is only appropriate to describe population growth for constant environmental conditions. Instead, modeling for changing temperature regimes can be achieved by rescaling chronological age to the number of degree-days (DD) required for each stage to develop into the next stage, also known as physiological age (Baskerville and Emin 1969, Andrewartha and Birch 1973) (Fig. 2).

The DD for each immature stage (e.g., egg, instar) is defined as the number of days it takes for an individual in that stage to develop at 1°C above the minimum temperature for development (MTD). The top row in Fig. 2 shows a typical stage-structured population model where transition probabilities from one stage to the next are constant and temperature-independent. In contrast, physiological ages are shown (7 and 6 DD for eggs and instar 1, respectively) in the middle row (Fig. 2). As temperature increases, for physiological ages, the transition probabilities move away from the diagonal of the transition matrix (Fig. 2, bottom). For example, an individual in physiological age 1 can “jump” directly to physiological age 3 (Fig. 2, middle row and bottom left matrix) in 1 d when temperature is  $T_1$  or 2°C above MTD (therefore, there will be transition probabilities for the jump from 1 to 3, 2–4, and so forth). In contrast, when temperature is higher ( $T_2$ , 4°C above MTD) an individual at physiological age 1 will jump to physiological age 5 in 1 d (middle row and bottom right matrix of Fig. 2). To implement this framework, we calculated the number of physiological ages immatures advance each day as  $\Delta T$  (difference between mean daily temperature  $T_k$

Table 1. Symbols for abbreviations and parameters used in the model

Abbreviation	
MTD	The minimum temperature at which viable development is possible
DD	Degree-days, or number of days required for a given immature stage to develop at 1 °C above MTD
DD <sub>T</sub>	Total number of days required for development from egg to adult eclosion at 1 °C above MTD
MTAP	Minimum temperature for population annual persistence ( $\lambda > 1$ )
MTSP	Minimum temperature for population seasonal persistence
AS	Number of adult age-classes
Symbols	
N	Population vector
A	Population transition matrix ( $DD_T + AS \times DD_T + AS$ )
I	Submatrix of A containing immature stages transition probabilities ( $DD_T \times DD_T$ )
F	Fertility row from A
C	Submatrix of A containing adult stage survival probabilities ( $AS \times AS$ )
$T_t$	Mean temperature at day <i>t</i>
$R_t$	Precipitation at day <i>t</i>
<i>n</i>	Number of immatures in a cavity
$S_{j,i}$	Daily baseline survival probability of any immature individual from physiological age <i>i</i> to physiological age <i>j</i> under no density dependence or rainfall dependence
$P_{j,i}$	Daily survival probability of any immature individual from physiological age <i>i</i> to physiological age <i>j</i> modified by density dependence and/or rainfall dependence
$F_a^k$	Number of eggs laid by a female mosquito of parous stage <i>k</i> and age <i>a</i>
$\phi$	Amount of daily precipitation required to maintain a breeding site full
$d_t(R_t)$	function that calculates at day <i>t</i> , the consecutive number of days in the past that had rained $R < \phi$ millimeters (or number of 'dry' days)
$\rho(d_t)$	calculates the probability of daily survival of an immature as a function of number of 'dry' days
$\omega$	Sensitivity of survival to the number of 'dry' days ( $d_t$ )
$D(n, \mu(i))$	Function that calculates the probability of survival as a function of the number of individuals <i>n</i> in a cavity
$\mu(i)$	Calculates the mortality rate as a function of the physiological age <i>i</i> of an immature
$\Psi$	Reduction in adult survival due to an extreme rainfall event

and MTD). Therefore, the position of the subdiagonal transition probabilities in the immature submatrix changes each day as a function of temperature, accelerating development when temperature is high and delaying it when closer to MTD (Fig. 2).

We used the physiological age of immatures to incorporate temperature dependence in the model. In contrast, adults were modeled using chronological age because there is conflicting information regarding the effects of temperature on adult mortality (Oda et al. 1999). The DD required for each immature stage of *Cx. quinquefasciatus* was calculated from data on developmental rate as a function of temperature in the laboratory (Rueda et al. 1990). These authors fit a nonlinear model for temperature and development

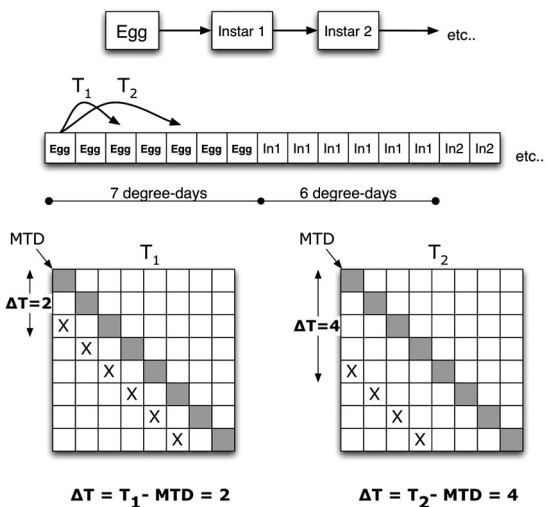


Fig. 2. Diagram illustrating the way temperature dependence was modeled. (Top row) Typical stage-structured model, where transition probabilities are temperature independent. (Middle row) Two stages might be modeled in physiological age units (eggs, 7 DD; and instar 1, 6 DD), where temperature  $T_1$  is 2 degrees above MTD and temperature  $T_2$  is 4 degrees above MTD. (Bottom row) Effect of temperature on the transition matrix (see explanation in text).

rate, which asymptotes at the extremes (between 10 and 15°C and 30 and 35°C). In Hawaii, mean daily temperature is bounded by a narrower range (between 12 and 24°C), which allowed us to fit the inverse of mean days to complete each life stage (developmental rate) as a linear function of temperature, substantially simplifying the model. The mean number of days to development for each stage were taken from Table 1 of Rueda et al. (1990), converted to developmental rates (by taking the inverse), and linear models were fitted to these data as a function of temperature ignoring the highest one (34°C). These lines were used to calculate DD for each of the stages (instar 1, instar 2, instar 3, instar 4, and pupae) (Table 2). We estimated an average MTD ( $\approx 10^\circ\text{C}$ ) for all immature stages from several populations of *Cx. quinquefasciatus* (Mogi 1992). The DD for eggs was set at 30 because it takes  $\approx 2$  d for *Cx. quinquefasciatus* eggs to hatch at  $\approx 25^\circ\text{C}$  (Hayes and Hsi 1975, Subra 1981). The dimensions of the immature projection submatrix (Fig. 1) were determined by the total DD required to complete all stages (179 DD). We used a baseline daily

Table 2. Estimated linear model parameters for development rates for different immature stages of *Cx. quinquefasciatus*

Stage	MTD (°C)	DD	R <sup>2</sup>
Instar 1	10.7	19	0.94
Instar 2	10.4	18	0.96
Instar 3	9.0	26	0.95
Instar 4	9.0	49	0.96
Pupae	7.5	37	0.87
All	9.9	137	0.91

**Table 3.** Proportion of cohort surviving ( $I_x$ ) and daily stage-specific survival probabilities ( $P_x$ ) according to a Gompertz survival model fitted by Clements and Paterson (1981)

Stage	$I_x$	$P_x$
nulliparous	1.00000	—
1-parous	0.47360	0.911
2-parous	0.13591	0.865
3-parous	0.01689	0.771
4-parous	0.00052	0.647

Average time between parous cycles was increased to 8 days.

probability of survival between physiological ages  $i$  and  $j = i + \Delta T$ ,  $S_{j,i}$ , as 0.9 (Hayes and Hsi 1975). This represents the daily survival of immatures in the absence of density dependence and rainfall dependence.

**Adult Survival and Fertility.** According to Clements and Paterson (1981), based on analysis of data collected by Samarawickrema (1967), *Cx. quinquefasciatus* females exhibit up to four gonotrophic cycles with an average duration of 3.5 d per cycle. However, our observations indicate that *Cx. quinquefasciatus* females require 6–8 d to complete a cycle: 1–2 d searching for a bloodmeal, 3–4 d digesting the bloodmeal and searching for an oviposition site, 1 d to oviposit and, two additional days recovering and searching for a new host. Although we used Clements and Paterson (1981) survivorship curves for daily survival rates, we increased the duration of the gonotrophic cycle to 8 d (Table 3). We used these parous-stage specific survival rates as the transition probabilities in the adult submatrix **C** (Fig. 1). To construct the transition matrix we used 33 adult age classes, eight for each of the parous stages 0–3 and one for parous stage 4 females (we assume these females die after oviposition). This arrangement allows us to keep track of behaviorally and ecologically distinct types of mosquitoes (e.g., mosquitoes that are biting hosts, or laying eggs) and makes the model adaptable for simulating transmission of diseases carried by *Cx. quinquefasciatus*.

*Cx. quinquefasciatus* egg rafts contain between 100 and 300 eggs (Mogi 1992). We assumed that females had a constant clutch of 150 eggs and that all females mated and found a blood meal in an optimistic scenario. The fertility row of the transition matrix (**F**) contains the fertilities of adult females at different daily stages. Because females do not reproduce continuously in time, these fertilities are distributed at 8-d intervals. The general form of the fertility vector is

$$\mathbf{F} = [0 \cdots F_9^1 \quad 0 \cdots F_{17}^2 \quad 0 \cdots F_{25}^3 \quad 0 \cdots F_{33}^4] \quad [2]$$

where  $F_a^P$  is the number of eggs laid by a female  $a$  days old and with parity  $P$ . In this model, we assumed ovipositing to be independent of rainfall (i.e., a female would lay in a cavity independent of how full it is), but we incorporate rainfall dependence in the mortality of immatures, which has the same demographic effect (see below).

**Rainfall Dependence.** Precipitation also affects the survival of immature and adult mosquitoes in both

field and laboratory experiments (Bradshaw and Holzapfel 1988, Mogi et al. 1996, Alto and Juliano 2001a). In Hawaii, annual rainfall varies among years and elevations (roughly between 2,000 and 5,000 mm) with most of the rain falling between November and March. Within a given year, lower elevations usually receive more rain than middle and higher elevations but this pattern is not consistent across years (NOAA 2003). Figure 3B compares mean monthly precipitation, from 1990 to 2003 for three climatic stations: Hilo International Airport (low elevation), Volcano National Park (middle elevation) and Kulani Camp (high elevation).

In Hawaiian forests, *Cx. quinquefasciatus* females lay their eggs in small-to-medium-sized tree holes or cavities. These cavities desiccate over extended periods of drought, making immature development sensitive to the lack of precipitation. At the other extreme, intense rainfall events can kill a large proportion of the adult population (Hayes and Downes 1980, LaPointe 2000). To model the effect of drought on immatures, we used the number of consecutive days up to time  $t$ ,  $d_t$  when rain was below a threshold ( $\phi$ ) for a single breeding cavity:

$$d_t(R_t) = (d_{t-1} + I_t)I_t \quad I_t = \begin{cases} 1 & R_t \leq \phi \\ 0 & \text{otherwise} \end{cases} \quad [3]$$

where  $R_t$  is the precipitation in day  $t$ , and  $I_t = 1$  if  $R_t \leq \phi$  and 0 otherwise. Then, the impact of drought on immature survival is a logistic function of  $d_t$ ,

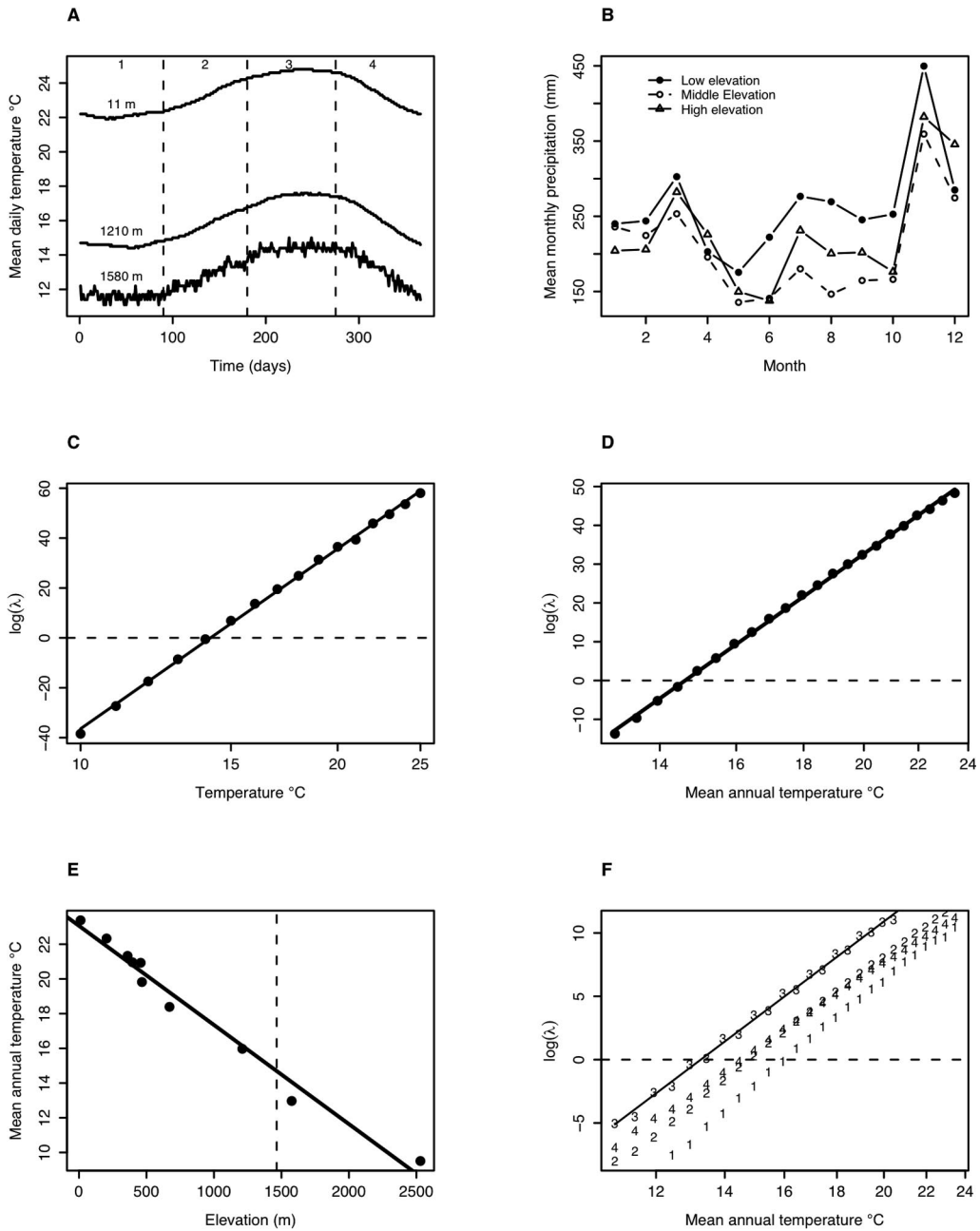
$$\rho(d_t(R_t)) = \frac{\exp(-\omega d_t(R_t))}{c + \exp(-\omega d_t(R_t))} \quad [4]$$

where  $\omega$  is a shape parameter controlling the sensitivity of  $\rho$  to  $d_t$  and  $c$  is a constant that assures that at small values of  $d_t$ ,  $\rho$  is close to 1. This function reduces the daily survival of immatures as the number of consecutive days without suitable rainfall (below  $\phi$ ) increases (Fig. 4A). Parameter  $\phi$  can be better grasped as the minimum amount of daily rain needed to keep a cavity full.

For adults, we modeled increased mortality in response to an extreme rainfall event. We defined an extreme rainfall event as >255 mm of cumulative rain throughout a period of 3 d ( $t - 2$ ,  $t - 1$ ,  $t$ ). In the model, adult survival was reduced to 5% of its original value at time  $t$  if the extreme rainfall condition was satisfied.

**Density Dependence.** Density-dependent competition can affect immature development rate for other mosquito species (Madder et al. 1983, Teng and Apperson 2000). For *Cx. quinquefasciatus*, we modeled density dependence on immature survival using an exponential function  $D_i(n)$  that reduced survival of a given physiological age  $i$  based on the number of individuals  $n$  in a breeding cavity. This functional form describes well the survival of immature *Aedes albopictus* (Skuse) and *Aedes triseriatus* (Say) at different densities in the laboratory (Teng and Apperson 2000). We assumed immatures in earlier stages of development were more sensitive to density dependence than





**Fig. 3.** (A) Average daily temperature between 1990 and 2003 for three sites at the east side of Mauna Loa, Hawaii. Four different seasons are separated by vertical dashed lines. (B) Mean monthly rainfall (1990–2003) at the same stations. (C) Relationship between temperature (°C) and population growth rate for a constant daily temperature regime. Log-log linear regression: intercept,  $-276.08$ ; slope,  $104.07$ ;  $R^2 = 0.998$ . (D) Relationship between temperature (°C) and population growth rate for the seasonal temperature regime. Log-log linear regression: intercept,  $-280.5$ ; slope,  $104.5$ ;  $R^2 = 0.999$ . (E) Relationship between elevation and mean annual temperature for stations on the east side of the Big Island of Hawaii. Linear regression: intercept,  $23.06$ ; slope,  $-0.00571$ ;  $R^2 = 0.978$ . The vertical dash line shows the maximum elevation at which the population can grow. (F) Relationship between temperature and the population growth rate ( $\lambda$ ) during four different seasons within a year (each number is a season). Log-log linear regression for summer: intercept,  $-68.6691$ ; slope,  $26.56$ ;  $R^2 = 0.998$ .

older individuals. We excluded eggs from density dependence, because egg survival and hatching are probably less dependent on egg density. The strongest

density dependence is experienced by the youngest instar 1 ( $i = 31$ ) and the weakest by the oldest pupae ( $i = 179$ ) (Fig. 4). We assumed the carrying capacity

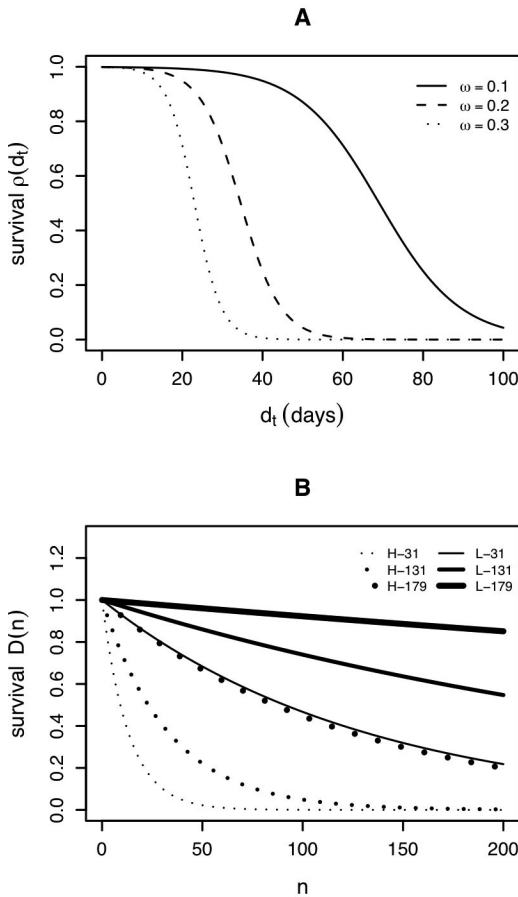


Fig. 4. (A) Survival of immatures as a function of the number of previous consecutive "dry" days (below a threshold  $\phi$ ) at different sensitivities to drought ( $\omega$ ). (B) Density-dependent survival ( $D$ ) for immatures as a function of the number of individuals in the cavity. Solid curves show the low (L) density-dependent scenario, and broken curves the high (H) density-dependent scenario. Curves are shown for each of three physiological ages  $i$ : 31 (instar 1), 131 (instar 3), and 179 (pupae).

of a typical cavity to be  $\approx 300$  individuals. The family of functions describing density-dependent survival is of the following form:

$$D_i(n) = \exp(-\mu(i)n) \quad [5]$$

where the intensity of mortality ( $\mu$ ) is a linear function of physiological age  $i$ ,

$$\mu(i) = ai + b \quad [6]$$

and  $a$  and  $b$  are constants that describe the change of  $\mu$  with physiological age. We considered two scenarios for density dependence: 1) low, where a 50% reduction in survival for the youngest instar 1 ( $i = 31$ ) occurred at a density of 30% of the carrying capacity of the cavity (or 91 individuals per cavity); and 2) high, where a 50% reduction in survival for the youngest instar 1 occurred at 3% carrying capacity (or nine individuals per cavity). Coefficients  $a$  and  $b$  changed

with each of these scenarios (low-density dependence:  $a = -4.6 \times 10^{-5}$ ,  $b = 0.00904$ ; high-density dependence:  $a = -4.6 \times 10^{-4}$ ,  $b = 0.0904$ ). Figure 4B illustrates several low- and high-density dependence curves for selected physiological ages.

**Elements of the Transition Matrix A.** Based on the above-mentioned considerations, the transition probabilities in matrix A are defined as follows. In the immature submatrix I, the transition probability  $P_{j,i}$  from physiological age  $i$  to  $j$  is given by

$$P_{j,i} = S_{j,i} \cdot \rho(d_i(R_i)) \cdot D(n, \mu(i)) \quad [7]$$

where  $S_{j,i}$  is the baseline survival probability for an immature that starts from physiological age  $i$  and moves to physiological age  $j$ , and  $\rho$  and  $D$  are the functions defining the probabilities of survival as a function of rainfall and density, respectively, for an individual in physiological age  $i$  (see equations 3–6).

Recall that the number of physiological ages moved in a day is temperature-dependent and given by  $\Delta T = T_t - \text{MTD}$ . Although the effect of temperature does not directly modify any of these survival terms, the probability of a particular immature surviving to the next immature stage is affected by temperature. For example, the expected proportion of instar 1 individuals dying before becoming instar 2 is  $[1 - (P_{j,i})^\delta]$ , where  $\delta$  is the expected number of days for an instar 1 individual to become an instar 2 (Fig. 2). The number of days is temperature-dependent and is  $\delta = (DD - 1)/\Delta T$ . If an instar 1 requires 18 DD, the proportion of individuals dying before instar 2 at  $\Delta T = 3$  is  $[1 - (0.9)^{17/3}] = 0.45$ . At a higher temperature ( $\Delta T = 6$ ), development occurs in a shorter time and the expected proportion of individuals dying before instar 2 is 0.25.

The daily survival probabilities of adult females from age  $a$  to age  $a + 1$  are given by

$$S_{a+1,a}^k = P_{a+1,a}^k \cdot I \cdot \Psi \quad [8]$$

where  $P_{a+1,a}^k$  is the baseline daily survival of adult females of parity  $k$  (from Table 3),  $I$  is an indicator variable that denotes an extreme rainfall event and  $\Psi$  is the reduction in survival due to this event (to 5% by default). In the absence of adequate information for *Cx. quinquefasciatus*, we assumed negligible effects of temperature on adult survival. Finally, the fertility of adult females of age  $a$  and parity  $k$  ( $F_a^k$ ) is a constant of 150 eggs.

The model equation (equation 1) describes the population dynamics of individuals breeding and emerging from a single cavity. We have made the provisional assumption that cavity size and carrying capacity are similar at all elevations. However, cavity size and availability for *Cx. quinquefasciatus* may vary within and between elevations, with land use, type of soil, pig density, and distance to nearest human habitation among other factors (LaPointe 2000; C. Atkinson, unpublished data). To estimate population dynamics from a larger geographic area, we would recommend estimates of cavity density and size along the elevational gradient. Currently, these data are not available, and our model cannot be reliably used to

estimate densities of *Cx. quinquefasciatus*. However, our model can be used to predict and compare the temporal dynamics of *Cx. quinquefasciatus* populations at different elevations, and it can be further refined to make density predictions as data on cavity availability and density become available.

**Model Analysis.** We used the model to address four questions regarding mosquito populations: 1) What is the long-term effect of temperature on the population dynamics?, 2) How do seasonal rainfall and temperature affect population dynamics?, 3) How does the inclusion of biotic effects (density dependence) change the dynamics of the system? and 4) How do elevational gradients in rainfall and temperature affect mosquito dynamics?

**Temperature Dependence.** The behavior of the model was analyzed under both constant and seasonal temperature regimes. In the constant regime, the mosquito population was allowed to grow at a constant daily temperature in the range between 10 and 25°C. The long-term dynamics of the model was assessed by calculating the population growth rate (dominant eigenvalue  $[\lambda]$  of the annual matrix) (Caswell 2001):

$$\mathbf{A}_y = \mathbf{A}_{365} \mathbf{A}_{364} \cdots \mathbf{A}_2 \mathbf{A}_1$$

where  $\mathbf{A}_i$  is the transition matrix of the model for day  $i$  and  $\mathbf{A}_y$  is the annual matrix (the cumulative matrix product of all daily matrices).

Three reference stations along the east side of Mauna Loa (Hilo, Volcano National Park and Kulani Camp) were used to determine the annual seasonal temperature regime along an elevational gradient between 0 and 2,500 m in elevation (Fig. 3A) by using average daily temperature data between 1990 and 2002 from the National Climatic Data Center (NOAA 2003). To calculate the population growth rate at other elevations, 22 annual temperature curves were constructed by adding (19 curves) or subtracting (three curves) 0.5°C increments to a smoothed curve for Kulani Camp (high elevation). To estimate the maximum elevation at which mosquitoes can persist, we used two regression analyses. The first regression between the average annual temperature for each of these curves and population growth rate predicted by the model, allowed us to estimate the mean annual temperature at which  $\lambda = 1$  (minimum temperature for annual persistence, MTAP). The second regression between mean annual temperature and elevation was fitted for climatic stations on the east side of the Island of Hawaii. This regression was used to calculate the elevation at which the MTAP occurred.

Because mosquitoes may move from lower to higher elevations, they may persist only during the warmest months at high elevations. Therefore, a similar analysis was performed to estimate the minimum temperature for seasonal persistence (MTSP) during four seasons of the year: January–March (“winter”), April–June (“spring”), July–September (“summer”), and October–December (“fall”) (Fig. 3A).

The estimation of  $\lambda$  at these elevations represent maximum potential population growth rate because

we assumed no density dependence and no rainfall dependence.

**Rainfall Dependence.** The effect of rainfall on mosquito population growth and dynamics was examined by finding isoclines of population growth along the two-dimensional parameter space of threshold rain ( $\phi$ ) and the sensitivity to drought ( $\omega$ ) at all three elevations (low, middle, and high). A potential limitation of this analysis is that the position of the growth isocline in parameter space changes within a given elevation if rainfall changes between years. To bracket the problem, we calculated two isoclines for each elevation corresponding to the wettest and driest year in Hawaii in the past 15 yr (1990: annual rain, 4,200–5,000 mm; 1995: annual rain, 1,800–2,200 mm) (NOAA 2003). This allows to narrow the region in parameter space where the growth isocline would lay most of the time within a given elevation. Isoclines were found by iterating through parameter space and calculating for each iteration the dominant eigenvalue  $\lambda$  of the annual matrix  $\mathbf{A}_y$ . Isoclines were constructed by linearly interpolating between boundary points (left of the point the population grows; right of it, it declines). Threshold rain ( $\phi$ ) was varied between 1 and 30 mm with a resolution of 0.5 mm and sensitivity to drought ( $\omega$ ) between 0.01 and 0.7 with a resolution of 0.01. Population predictions for each year and each elevation were constructed by running the model by using a combination of  $\phi$  and  $\omega$  that would allow growth in both wet and dry years (on the left side of the isoclines). Populations were started with 10 individuals in each physiological and age class and a low level of density dependence (50% reduction in survival for the youngest instar 1 at a density of 30% of the carrying capacity of the cavity). Populations were simulated for 5 yr, but only the last year is evaluated to avoid transient dynamics.

**Density Dependence.** The effect of density dependence was examined by running population projections at three elevations and varying the level of density dependence (low versus high) while maintaining other model parameters constant. Daily rainfall and temperature for a 15-yr period (1985–2000) at the three elevations were obtained from the National Climatic Data Center (NOAA 2003). Projections were run for this 15-yr period but for clarity only 3 yr are shown (1990–1992).

**Model Validation.** Population projections from the model were compared with mosquito trap data collected at three study sites from the east side of Mauna Loa, Hawaii: Bryson’s (300-m elevation), Crater rim (1,200 m), and C.J. Ralph (1,800 m). These sites are fairly representative of relatively forested habitat at each elevation. From June 2002 until December 2003, every 4 wk at each site, trap stations were established every 100 m along five, 1-km transects resulting in 45 possible trap locations on each of the three sites. For each trapping session, five stations along each transect were randomly chosen, and one CO<sub>2</sub>-baited trap and one oviposition trap were operated at those sites for four nights, resulting in a total of 100 trap-nights (TN). CO<sub>2</sub> traps are miniature CDC light traps (J.W. Hock

Company, Gainesville, FL) modified to operate without the light or rain lid. The source of CO<sub>2</sub> is a 350-g block of dry ice housed in a small, insulated food container. Live mosquitoes were retrieved from traps each morning, identified, and brought back to the laboratory for dissection. Mosquito abundance is expressed as number of adult mosquitoes trapped per 100 TN.

To compare the model with the available data at each elevation, rainfall from a nearby weather station, Bryson's (Hilo International Airport), Crater rim (Volcano National Park), and C.J. Ralph (Kulani Camp) was used to produce results. We are confident rainfall estimates from these weather stations are representative of the rainfall experienced at the mosquito sampling sites, because rainfall tends to be more spatially clustered and does not vary as consistently with elevation compared with temperature. However, temperature for the mosquito stations was extrapolated when the nearest weather station, and sampling stations were at different elevations (Bryson's and C.J. Ralph) by using the procedure described in a previous section (see Model Analysis/Temperature Dependence). The model was run for each study site from 1990 to 2003 and fitted to the data. Model fit was achieved by choosing the parameter values for threshold rain ( $\phi$ ) and sensitivity to drought ( $\omega$ ) that minimized the sum of the squared difference between mosquito abundance data of each data point and model prediction (least squares estimator). This was achieved by using the numerical algorithm *nlm()* in the program R (R Development Core Team 2003). The proportion of data variance explained by the model ( $R^2$ ) was calculated as an indicator of the agreement.

## Results

**Effects of Temperature.** Fig. 3C shows the effect of constant daily temperature on the annual population growth of mosquitoes. As expected, population growth rate increases exponentially with temperature. However, the estimated minimum temperature for annual persistence, MTAP, is well above the minimum developmental temperature, MDT (MTAP, 14.2°C; MDT, 10°C). A similar growth pattern was observed for seasonal temperatures (Fig. 3D). However, MTAP was slightly larger for the seasonal model compared with the constant model (14.64°C). Based on the seasonal model, we estimated the maximum elevation at which mosquitoes can persist on the Island of Hawaii to be  $\approx 1,475$  m (Figs. 3E and 5). However, if mosquitoes migrate from middle elevations, populations could persist at higher elevations during the warmest season of the year. Seasonal persistence would occur at elevations where average seasonal temperature exceeds 13.2°C (Fig. 3F), and mosquito range could extend to 1,715 m during the summer (July–September) (Fig. 5). However, these estimates do not consider density dependence, rainfall, or host limitation, which should reduce potential growth and population persistence.

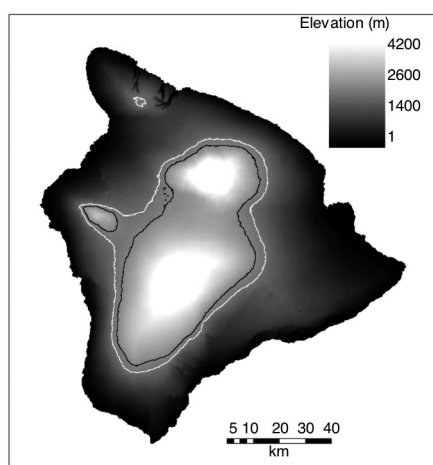


Fig. 5. Digital elevation map of the Island of Hawaii showing the maximum elevation at which mosquitoes can persist on an annual basis (white line) and during the summer period (dark line).

The temporal dynamics of mosquito populations vary among elevations (Fig. 6). With low-density dependence, populations cycle at two different scales: a long-term annual cycle, which peaks near the end of the year, and a series of intra-annual cycles. The annual cycles are driven by seasonal changes in temperature and rainfall and their amplitude decreases with elevation. The annual cycles are less evident at low elevation, and the population seems more erratic (Fig. 6). As expected, high-density dependence reduced population size, but it did not affect the population cycling pattern. The intra-annual cycles are a result from within-cavity dynamics and more pronounced with elevation (see *Discussion*).

**Effects of Rainfall.** The effects of rainfall on the mosquito population dynamics at different elevations are shown in Fig. 7. Because the effect of rainfall on immature survival was modeled as an interaction between two parameters (minimum daily rain needed to keep a cavity full [ $\phi$ ] and reduction of immature survival from drought [ $\omega$ ]), we analyzed how combinations of these parameters affected population growth in the absence of density dependence for three different elevations under two rainfall regimes (a wet year, 1990, and a dry year, 1995). Regions in parameter space where mosquito population growth was possible ( $\lambda \geq 1$ ) are to the left of the isocline, whereas combinations of parameters that resulted in population decline ( $\lambda < 1$ ) are to the right of the isocline.

At all elevations, population growth occurred when threshold rain was low (independent of drought sensitivity) or high (at very low drought sensitivity) (Fig. 7). Biologically, this means that population growth can occur under a range of rainfall conditions. On one side of this spectrum, with sufficient daily rainfall to keep a cavity full ( $\phi$ ) population growth occurs independently from the sensitivity of immatures to drought ( $\omega$ ). On the opposite side of this spectrum, population growth could occur with low rainfall, but only when



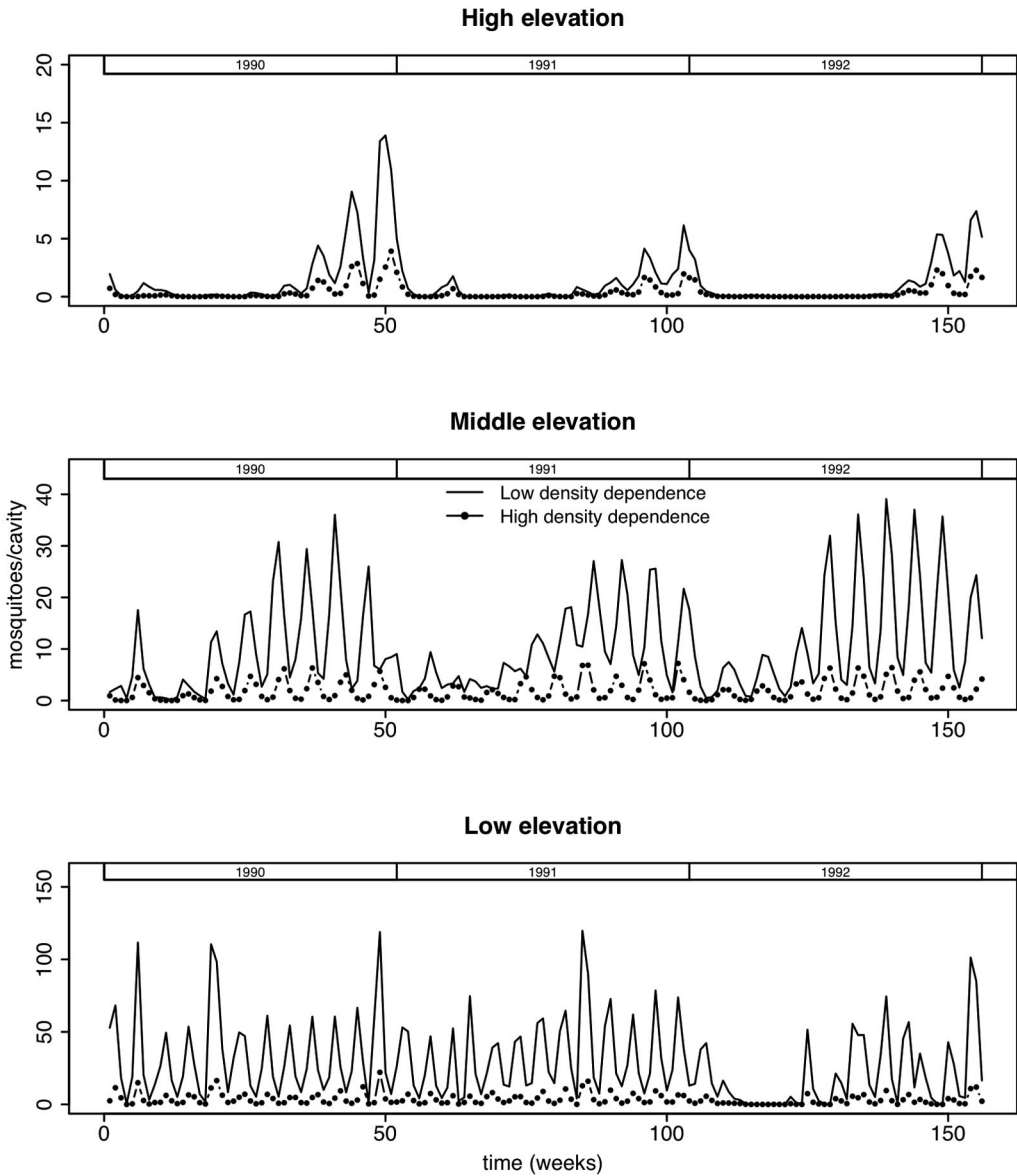
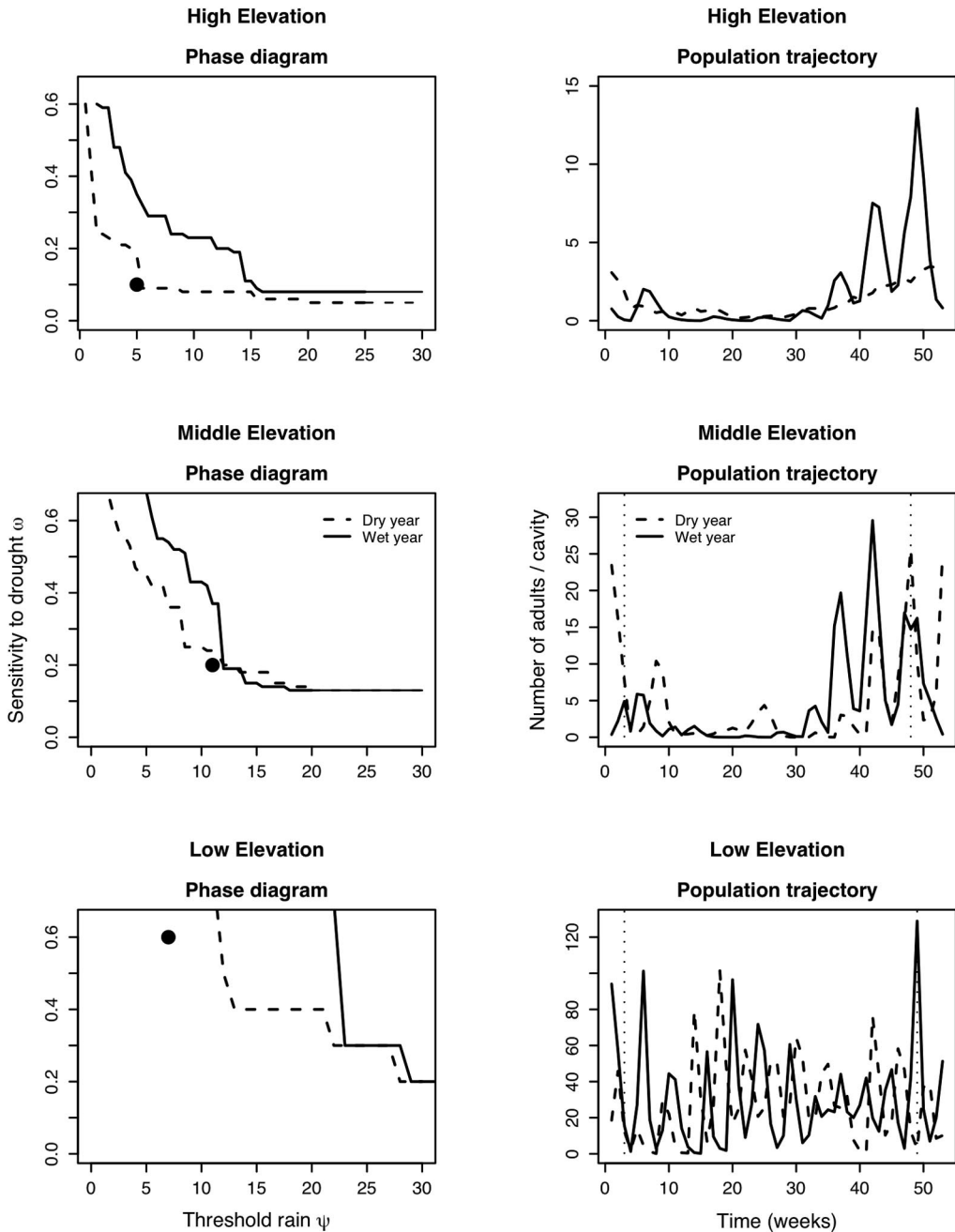


Fig. 6. Population projections of mosquitoes at three different elevations under low- and high-density dependence (high elevation, 1,580 m; middle elevation, 1,200 m; and low elevation, 11 m). Projections were started in 1988 to allow for transient dynamics with 10 individuals in each physiological age and adult age class. The parameters used where  $\phi = 5$  and  $\omega = 0.1$  for all elevations.

the sensitivity of immatures to drought is low. In Hawaii, these parameters will likely interact with the frequency of different cavity types and their characteristics. Small cavities (tree holes, lava crevices, and cemetery vases) are ephemeral but important if sufficient rain falls. Intermediate-sized breeding cavities (pig-created tree fern cavities) are less dependent on daily rainfall but are more susceptible to prolonged drought, whereas large cavities (barrels and water holes) can survive prolonged periods of drought but are only seasonally filled.

At higher elevation, the combination of parameters favorable for population growth (area under the isoclines) decreases. This is a result of the temperature and rainfall at different elevations. At higher elevation, it is colder and immatures take longer to reach the adult stage. This, in conjunction with the drier conditions, also requires immatures to develop in cavities that have sufficient water or to have a very low sensitivity for drought. At the other extreme, at low elevations, temperature and rainfall are higher and immatures take a shorter time to develop. This allows



**Fig. 7.** Isoclines of population growth (left column) as a function of threshold daily rain and sensitivity to drought for an extreme dry year (1995, broken lines) and an extreme wet year (1990, solid lines) at three elevations (same as Fig. 6). The dots in each graph represent a particular combination of parameters used to run population projections (right column). A week where an extreme rainfall event occurred is shown as a vertical dotted line. All simulations were run under low-density dependence, started with 10 individuals in each class and run for two previous years to allow for transient dynamics.

them to reach adulthood under a wider variety of cavity sizes and drought tolerances. The situation at middle elevation is intermediate and may vary based on annual weather patterns (Fig. 7).

At all elevations, parameter space for population growth (under the isocline) is larger in a wet year

(1990) than in a dry year (1995). This comparison effectively isolates the effects of temperature from those of rainfall, because daily mean temperature difference between dry and wet years were small at all elevations (mean  $\pm$  95% CI: low elevation,  $0.75 \pm 0.135^\circ\text{C}$ ; middle elevation,  $0.41 \pm 0.202^\circ\text{C}$ ; and high

elevation,  $-0.16 \pm 0.220^{\circ}\text{C}$ ). To develop into adults in a dry year, immatures would need 1) smaller cavities that fill up more quickly with the available rain, or 2) large enough cavities that resist prolonged droughts. The availability and viability of these different cavity types will likely change with elevation.

The potential impact of these contrasting rainfall conditions on the population dynamics of mosquitoes for all elevations is shown on the right column of Fig. 7. For a high elevation site, a dry year has a dramatic impact on mosquito populations, especially late in the year. However, this effect is not so clear for middle- and low-elevations sites. Although total population size is smaller in the dry year than in the wet year, catastrophic rainfall events can increase the mortality of adults during wet years (dotted vertical lines in right column of Fig. 7).

**Model Validation.** Model results for 2002–2003 showed a reasonable agreement with available mosquito data at three different elevations (Fig. 8). The high elevation station (C.J. Ralph, 1,800 m) is above the expected distribution of mosquitoes predicted by our model, and no mosquitoes were trapped during most sessions with a maximum of two individuals/100 TN. At middle elevation the model predictions replicated observed seasonal dynamics, explaining  $\approx 75\%$  of the variance observed in the data. At low elevation, the model predictions were out of phase with the seasonal dynamics in 2002, but consistent with 2003 observations, explaining  $\approx 41\%$  of the variance in the data.

### Discussion

Although the seasonal nature of our model (transition matrix is not constant through time) prohibited a formal sensitivity analysis of the parameters (Caswell 2001), several major conclusions can be drawn from the analyses presented here. First, temperature is likely the major driving force behind mosquito population growth and abundance in Hawaii, especially across different elevations. Second, rainfall dependence imposes important constraints on population size, which are especially evident during dry years. Third, seasonal climatic forcing and density dependence for immature mosquitoes create annual population cycles of mosquitoes. These cycles vary by elevation and loosely follow the annual temperature with peak populations later in the year. Fourth, density dependence for immature mosquitoes can affect population size without altering the seasonal dynamics. Finally, the seasonal population dynamics predicted by the model at all elevations is consistent with the available field data.

**Temperature Dependence.** Even with no rainfall dependence or density dependence, our model predicts that *Cx. quinquefasciatus* populations cannot be sustained at elevations above 1,475 m above sea level. In the summer (July–September) mosquitoes could occur at elevations up to 1,715 m, but these populations would not be able to persist during the cooler fall, winter, or spring. The model predicted no mosquitoes at the highest elevation site, C.J. Ralph, which is  $\approx 350$

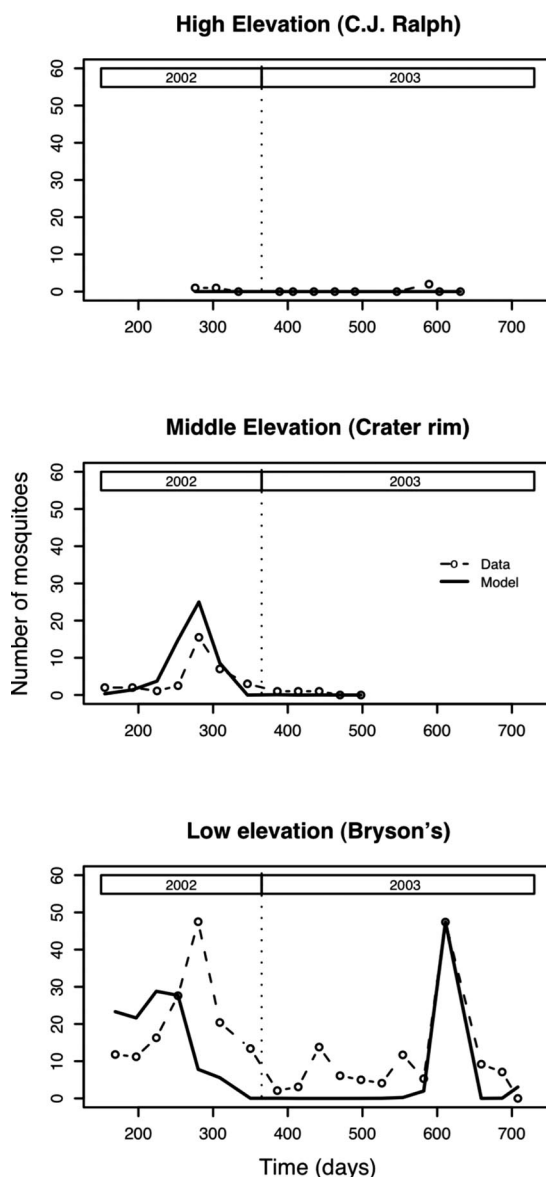


Fig. 8. Comparison of number of adult *Cx. quinquefasciatus* per 100 trap nights (open circles and lines) with model fits (solid lines) at each of three different elevations: C.J. Ralph (1,800 m), Crater rim (1,200 m), and Bryson's (280 m). Time is measured as the number of days since 1 January 2002. Dotted vertical line indicates the end of 2002. At the highest elevation, the model predicts no mosquitoes, so no climatic stations were used for the fit. Best fit parameters and  $R^2$ : middle elevation,  $\phi = 5$ ,  $\omega = 0.342$ ,  $R^2 = 0.75$ ; and low elevation,  $\phi = 6$ ,  $\omega = 0.716$ ,  $r^2 = 0.41$ .

m and 100 m above the predicted annual and summer ranges, respectively. Only four mosquitoes were captured at this site during 1,087 TN between 10 March 2002 and 23 September 2003. Two of these individuals were captured in the summer (August) and two in the late summer-early fall (October) when mosquitoes were predicted to occur at 1,700 m (Fig. 5). These

observations are consistent with our model predictions, and although it is possible that a very small resident population of *Cx. quinquefasciatus* persists at C.J. Ralph, it is more likely these individuals moved up the mountain from a neighboring lower elevation as seasonal visitors.

These elevational distributions of mosquitoes have important implications for the management of diseases carried by *Cx. quinquefasciatus* in Hawaii. Our model predicts mosquito populations should be able to persist at the 14.6°C annual temperature isocline and as a summer population at the 13.2°C isocline. However, Benning et al. (2002) reported the minimum temperature for development of avian malaria oocysts in adult *Cx. quinquefasciatus* is 13°C and peak *Plasmodium* prevalence is observed in mid-elevation forests where annual temperatures are  $\approx 17^\circ\text{C}$ . These results suggest that *Cx. quinquefasciatus* living at higher elevations would not be likely to transmit avian malaria at high rates. However, if annual temperature increased by 2°C due to global warming or other factors, this picture would radically change (Benning et al. 2002).

**Rainfall Dependence.** The effect of rainfall as a limiting factor in mosquito populations further restricts population growth and population size in our model (Fig. 7). Rainfall dependence was modeled as the interaction between two parameters: the minimum amount of daily rain needed to maintain breeding sites ( $\phi$ ) and the sensitivity of immatures to mortality from drought ( $\omega$ ). This sensitivity also can be equated with evaporation rate from a breeding cavity; at high temperatures, evaporation will be higher than at low temperatures for cavities of the same volume and surface area. At low values of  $\phi$ , a fairly small amount of rain is sufficient to keep a breeding site full of water, allowing the population to grow at a wide range of drought sensitivities ( $\omega$ ). However, as  $\phi$  increases, more rain is needed to maintain breeding sites and population growth is only possible when drought sensitivity is relatively low. The position of the population growth isocline, however, is strongly dependent on elevation. At high elevations, immature mosquitoes develop at a slower rate and likely require small breeding sites that need minimal rain to remain full, or large breeding sites with more water that are fairly insensitive to drought. In contrast, at lower elevations the isocline moves further to the right, allowing a larger range of breeding sites and drought sensitivities. For all elevations, a dry year moves this isocline to the left, limiting the range of rainfall parameters for successful population growth (Fig. 7).

Although additional field data are needed to refine model parameters, patterns from the model can be used to evaluate potential control strategies for breeding mosquitoes at different elevations. The main breeding sites used by *Cx. quinquefasciatus* in Hawaii are tree holes, pig-created tree fern cavities, wallows, and a variety of human-made cavities (LaPointe 2000). Desiccation dynamics is affected by the surface-to-volume ratio of a cavity and temperature (Kingsolver 1979). Breeding sites with relatively high

surface-to-volume ratios (wallows and to some extent tree fern cavities) have high evaporation rates and would not be good breeding sites at low elevation during the dry season. At high elevations they would provide suitable habitats for breeding because the lower temperatures prevent their rapid desiccation. In contrast, at lower elevations, breeding sites with low surface-to-volume ratios (tree holes, cemetery vases, other human-made conical or cylindrical shaped cavities) will dry more slowly at the high temperatures. Based on this argument, potential control strategies at high and middle elevations could focus on cavities with a wide range of surface to volume ratios, whereas at low elevations the focus should be on cavities that resist desiccation during the dry periods of the year.

**Population Dynamics and Density Dependence.** Density dependence for immature mosquitoes stabilized population growth and contributed to annual cycles in the mosquito population. The strength of density dependence affects overall population size, but not the seasonal population cycles (Fig. 6). The shape and amplitude of the annual cycle also differed between elevations. At high elevation, mosquito numbers were low and peaked during the late summer and early fall. At middle elevation, mosquito numbers are higher with a longer season of population peaks during summer-fall. At low elevation, mosquito numbers were the highest and the annual cycle is more difficult to discern with a more erratic population trajectory throughout the year.

Whether density dependence occurs in the breeding cavities of *Cx. quinquefasciatus* in Hawaii requires further investigation. However, density dependence is common in other mosquito species such as *Ae. albopictus* and *Ae. triseriatus* and sensitive to temperature (Teng and Apperson 2000). In these species, survival declined as much as 80% when density reached 200 individuals per cavity in the laboratory. Whether within-cavity density-dependent mortality of larvae and pupae occurs in natural populations of *Cx. quinquefasciatus* in Hawaii remains undocumented. Further research is needed to determine the relationship between temperature and density-dependent mortality in *Cx. quinquefasciatus* in Hawaii.

**Model Validation.** Although our model was not built to predict mosquito abundance per se, it adequately captures field data for the east side of Mauna Loa (Fig. 8). The model predicted  $\approx 40\%$  of the variance in numbers of mosquitoes trapped in Bryson's (low elevation) and  $\approx 75\%$  of the variance at Crater rim (middle elevation). These results are encouraging because the model replicates most of the temporal population patterns observed at different elevations. At present, our model may have limited ability to accurately predict mosquito numbers because breeding site availability has not been explicitly modeled. Large spatial variation in breeding site availability and cavity size between habitats or along the elevational gradient may influence population size without affecting the annual cycles. With these caveats, the model reproduces the relative seasonality expected at different



elevations, and inclusion of other variables will further improve these predictions.

**Future Directions.** Our model does not currently include other ecological aspects that may be important in understanding the dynamics of *Cx. quinquefasciatus* populations in the forest ecosystems of Hawaii. For example, temperature dependence could be enhanced by incorporating potential effects of temperature on adult survival and reproduction or by refining data for immature stages. Density dependence, in conjunction with seasonal climate variation, seems to be an important driver of mosquito dynamics, and additional field data would refine parameters and enhance model predictions. The explicit inclusion of cavity availability will allow the model to give more accurate predictions in heterogeneous landscapes.

In addition, further model development is needed to 1) incorporate the influence of temperature on parasite development within the vector, 2) assess the effects of long-term climate change on mosquito population dynamics, and 3) integrate disease transmission dynamics for avian malaria and pox in Hawaii. Our objective is not only provide a detailed understanding of the factors underlying mosquito population dynamics in Hawaii but also to provide a template for model development of other species of mosquitoes in other ecosystems. A similar approach would be particularly useful for other mosquito-borne diseases such as West Nile virus that are an increasing threat for human and wildlife health.

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### References Cited

- Alto, B., and S. Juliano. 2001a. Precipitation and temperature effects on populations of *Aedes albopictus* (Diptera: Culicidae): implications for range expansion. *J. Med. Entomol.* 38: 646–656.
- Alto, B., and S. Juliano. 2001b. Temperature effects on the dynamics of *Aedes albopictus* (Diptera: Culicidae) populations in the laboratory. *J. Med. Entomol.* 38: 548–556.
- Andrewartha, H. G., and L. C. Birch. 1973. The history of insect ecology, pp. 229–266. *In* R. F. Smith, T. E. Mittler, and C. N. Smith [eds.], *History of entomology*. Annual Reviews, Inc., Palo Alto, CA.
- Atkinson, C. T., K. L. Woods, R. J. Dusek, L. S. Sileo, and W. M. Iko. 1996. Wildlife disease and conservation in Hawaii: pathogenicity of avian malaria (*Plasmodium relictum*) in experimentally infected Iiwi (*Vestiaria coccinea*). *Parasitology* 111: S59–S69.
- Baskerville, G. L., and P. Emin. 1969. Rapid estimation of heat accumulation from maximum and minimum temperatures. *Ecology* 50: 514–517.
- Benning, T. L., D. LaPointe, C. A. Atkinson, and P. M. Vitousek. 2002. Interactions of climate change with biological invasions and land use in the Hawaiian islands: modelling the fate of endemic birds using a geographical information system. *Proc. Natl. Acad. Sci.* 99: 14246–14249.
- Bradshaw, W. E., and C. M. Holzapfel. 1988. Drought and the organization of tree-hole mosquito communities. *Oecologia (Berl.)* 74: 507–514.
- Caswell, H. 2001. *Matrix population models*. Sinauer Publishers, Sunderland, MA.
- Clements, A. N., and G. D. Paterson. 1981. The analysis of mortality and survival rates in wild populations of mosquitoes. *J. Appl. Ecol.* 18: 373–399.
- Gubler, D. J. 1966. A comparative study of on the distribution, incidence and periodicity of the canine filarial worms *Dirofilaria immitis* Leidy and *Dipetalonema reconditum* Grassi in Hawaii. *J. Med. Entomol.* 3: 159–167.
- Hardy, D. E. 1960. *Insects of Hawaii*, vol. 10. University of Hawaii Press, Honolulu, HI.
- Hayes, J., and B. P. Hsi. 1975. Interrelationships between selected meteorologic phenomena and immature stages of *Culex pipiens quinquefasciatus* Say: study of an isolated population. *J. Med. Entomol.* 12: 299–308.
- Hayes, J., and T. M. Downes. 1980. Seasonal changes of an isolated population of *Culex pipiens quinquefasciatus* (Diptera: Culicidae): a time series analysis. *J. Med. Entomol.* 17: 63–69.
- Henshaw, H. W. 1902. *Birds of the Hawaiian possessions with notes on their habitats*. T. G. Thrum, Honolulu, HI.
- Kingsolver, J. G. 1979. Thermal and hydric aspects of environmental heterogeneity in the pitcher plant mosquito. *Ecol. Monogr.* 49: 357–376.
- LaPointe, D. 2000. *Avian malaria in Hawaii: the distribution, ecology and vector potential of forest-dwelling mosquitoes*. Ph.D. thesis, University of Hawaii, Honolulu, HI.
- Madder, D., G. Surgeoner, and B. Helson. 1983. Number of generations, egg production and developmental time of *Culex pipiens* and *Culex restuans* (Diptera: Culicidae) in southern Ontario. *J. Med. Entomol.* 20: 275–287.
- Mogi, M. 1992. Temperature and photoperiod effects on larval and ovarian development of New Zealand strains of *Culex quinquefasciatus* (Diptera: Culicidae). *Ann. Entomol. Soc. Am.* 85: 58–66.
- Mogi, M., I. Miyagi, and K. Abadi. 1996. Inter and intraspecific variation in resistance to desiccation by adult *Aedes (Stegomyia)* spp. (Diptera: Culicidae) from Indonesia. *J. Med. Entomol.* 33: 53–57.
- [NOAA] National Oceanic and Atmospheric Administration. 2003. National Climatic Data Center, <http://www.ncdc.noaa.gov/oa/ncdc.html>.
- Oda, T., K. Uchida, A. Mori, M. Mine, E. Y., K. Kurokawa, K. Kato, and H. Tahara. 1999. Effects of high temperature on the emergence and survival of adult *Culex pipiens molestus* and *Culex quinquefasciatus* in Japan. *J. Am. Mosq. Control Assoc.* 15: 153–156.
- R Development Core Team. 2003. *A language and environment for statistical computing*. Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org>, ISBN 3-900051-00-3.
- 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.

- Samarawickrema, W. A. 1967. A study of the age composition of natural populations of *Culex pipiens fatigans* Wiedemann in relation to the transmission of filariasis due to *Wuchereria bancrofti* (Cobbold) in Ceylon. Bull. World Health Organ. 37: 117–137.
- Subra, R. 1981. Biology and control of *Culex pipiens quinquefasciatus* Say 1823 (Diptera, Culicidae) with special reference to Africa. Insect Sci. Appl. 1: 319–338.
- Teng, H., and C. Apperson. 2000. Development and survival of immature *Aedes albopictus* (Diptera: Culicidae) in the laboratory: effects of density, food and competition on response to temperature. J. Med. Entomol. 37: 40–52.
- Tripathy, D. N., W. M. Schnitzlein, P. J. Morris, D. L. Janssen, J. K. Zuba, G. Massey, and C. T. Atkinson. 2000. Characterization of poxviruses from forest birds in Hawaii. J. Wildl. Dis. 36: 225–230.
- van Riper, C. I., S. G. van Riper, M. L. Goff, and M. Laird. 1986. Epizootiology and ecological significance of malaria in Hawaiian land birds. Ecol. Monogr. 56: 327–344.
- van Riper, C. I., S. G. van Riper, and W. R. Hansen. 2002. Epizootiology and effect of avian pox on Hawaiian forest birds. The Auk 119: 929–942.
- Warner, R. E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. Condor 70: 101–120.

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