



Hot temperatures can force delayed mosquito outbreaks via sequential changes in *Aedes aegypti* demographic parameters in autocorrelated environments



Luis Fernando Chaves^{a,b,c,*}, Thomas W. Scott^{d,e}, Amy C. Morrison^d, Takenori Takada^c

^a Institute of Tropical Medicine (NEKKEN), Nagasaki University, 1-12-4 Sakamoto, Nagasaki 852-8523, Japan

^b Programa de Investigación en Enfermedades Tropicales, Escuela de Medicina Veterinaria, Universidad Nacional, P.O. Box 304-3000, Heredia, Costa Rica

^c Graduate School of Environmental Sciences, Hokkaido University, Sapporo 060-0810, Japan

^d Department of Entomology, University of California, Davis, CA 95616, USA

^e Fogarty International Center, National Institutes of Health, Bethesda, MD 20892, USA

ARTICLE INFO

Article history:

Received 23 August 2012

Received in revised form 6 February 2013

Accepted 28 February 2013

Available online 26 March 2013

Keywords:

Population delay
Density dependence
Climate change
Trade-offs
Lefkovich matrix

ABSTRACT

Aedes aegypti L. (Diptera: Culicidae) is a common pantropical urban mosquito, vector of dengue, Yellow Fever and chikungunya viruses. Studies have shown *Ae. aegypti* abundance to be associated with environmental fluctuations, revealing patterns such as the occurrence of delayed mosquito outbreaks, i.e., sudden extraordinary increases in mosquito abundance following transient extreme high temperatures. Here, we use a two-stage (larvae and adults) matrix model to propose a mechanism for environmental signal canalization into demographic parameters of *Ae. aegypti* that could explain delayed high temperature induced mosquito outbreaks. We performed model simulations using parameters estimated from a weekly time series from Thailand, assuming either independent or autocorrelated environments. For autocorrelated environments, we found that long delays in the association between the onset of “hot” environments and mosquito outbreaks (10 weeks, as observed in Thailand) can be generated when “hot” environments sequentially trigger a larval survival decrease and over-compensatory fecundity increase, which lasts for the whole “hot” period, in conjunction with a larval survival increase followed by a fecundity decrease when the environment returns to “normal”. This result was not observed for independent environments. Finally, we discuss our results implications for prospective entomological research and vector management under changing environments.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Aedes aegypti (L.) (Diptera: Culicidae) is one of the most common mosquitoes biting humans in many tropical cities. It is also a vector of viruses causing several major neglected tropical diseases such as dengue, Chikungunya and Yellow Fever (Gubler, 1989). The success of *Ae. aegypti* in urban environments is due to the abundance and suitability of larval habitats, i.e., artificial water containers (Schneider et al., 2004), and resources for reproduction, such as blood from human hosts (Harrington et al., 2001). *Ae. aegypti* populations are also sensitive to changes in the external environment. For example, eggs diapause and only hatch when humidity is very high or after they become submerged in water (Reiter, 2007), and like other insects, their developmental rate is a function of temperature (Christophers, 1960). Moreover, several long-term studies on

Ae. aegypti abundance have shown the abundance of this mosquito species to be correlated with different environmental factors, primarily rainfall and temperature (Barrera et al., 2011; Dibo et al., 2008; Foo et al., 1985; Ho et al., 1971; Oo et al., 2011; Schultz, 1993; Scott et al., 2000; Tonn et al., 1970), but also with “socio-ecological” factors such as unreliable water supply (Barrera et al., 1993; Padmanabha et al., 2010) or lack of community engagement in proper water container disposal (Predescu et al., 2007). Similar patterns of association between mosquito abundance and weather fluctuations have been observed in other *Aedes* spp. (Ho et al., 1971; Makiya, 1974; Sota et al., 1992), culicine (Barker et al., 2010; Hayes & Downs, 1980; Makiya, 1973) and anopheline (Minakawa et al., 2002) mosquitoes, as well as other Diptera vectors of disease (Morrison et al., 1995; Salomon et al., 2004). One of the intriguing patterns in these associations is the emergence of relatively long delays in the association between environmental changes and the occurrence of vector outbreaks. For example, in our previous study we found a 10 week delay between extreme high temperature and the occurrence of *Ae. aegypti* outbreaks, i.e., for the occurrence of abrupt increases in mosquito abundance (Chaves et al., 2012). A

* Corresponding author at: Institute of Tropical Medicine (NEKKEN), Nagasaki University, 1-12-4 Sakamoto, Nagasaki 852-8523, Japan. Tel.: +81 80 3262 2962.

E-mail addresses: lchaves@nagasaki-u.ac.jp, lchaves@umich.edu (L.F. Chaves).

plausible explanation for the occurrence of delayed mosquito outbreaks following extreme weather events is the canalization of environmental variability on population dynamics via changes in organism biology (e.g., development and physiology). These individual level changes can drive the dynamics of population level demographic parameters as a strategy to cope with challenges arising from a changing environment (Levins, 1968; Schmalhausen, 1949; Tuljapurkar, 1989). Here, we use a simple two-stage (larvae and adult) matrix model to ask if demographic changes associated with particular environmental conditions could explain the delayed association between temperature and *Ae. aegypti* population outbreaks. We simulate the model using parameter estimated from a time series from Thailand (Chaves et al., 2012) and evaluate a series of sequential changes in demographic parameters for a stochastic environment alternating between ‘normal’ and ‘hot’ conditions. Thus, unlike our previous work, where an additive forcing function explained mosquito outbreaks (Chaves et al., 2012), here we try to understand the emergence of mosquito outbreaks as consequence of changes in *Ae. aegypti* demographic parameters that could be triggered by the occurrence of unusual autocorrelated environments. We found that a 10-week lag maximum cross correlation, as observed in Thailand (Chaves et al., 2012), is more likely to emerge in auto-correlated environments following sequential changes in larval survival and adult fecundity, which decrease and increase, respectively, when the environment is ‘hot’. We conclude by discussing the importance of autocorrelated environments for *Ae. aegypti* population outbreaks, the potential implications of changes in individual mosquito traits, specially body size (Morales Vargas et al., 2010), on the demographic changes we assumed to recreate the mosquito population outbreaks, and the implications of our results for mosquito population management in changing environments.

2. Materials and methods

2.1. Data

Weekly mosquito density (N_t) time series data (Fig. 1A) were obtained by averaging *Ae. aegypti* abundance from 10 houses (out of a total of 23 monitored houses) in Village 6 (13° 38' N, 101° 18' E) of Hua Samrong Tambon (subdistrict), Plaeng Yao Amphoe (county), Chachoengsao (province) in Thailand using modified vacuum cleaners from June 1990–May 1993 (Scott et al., 2000). Samples were restricted to houses because this is the main resting habitat of adult *Ae. aegypti* (Christophers, 1960; Scott et al., 2000). Maximum Temperature (TMAX) data (Fig. 1B) were obtained from a weather station within a 20 KM radius of the site. We focus our analysis on TMAX based in our previous results, which indicated a major role for this climatic variable to explain *Ae. aegypti* population dynamics in Thailand (Chaves et al., 2012). Seasonal patterns of rainfall and temperature range in Thailand were within the range of recorded variability for the area (Chaves et al., 2012). See Scott et al. (2000) for further details on study sites, sampling, and time series data.

2.2. Time series descriptive statistical analysis

We examined the correlation structure of N_t and TMAX time series data using standard techniques for time series analysis (Shumway & Stoffer, 2000). These included the autocorrelation function, ACF, the Partial ACF, PACF, (Fig. S1) and the cross-correlation function, CCF, of TMAX pre-whitened residuals with residuals from a second order autoregressive model; i.e., with two time lags based on the ACF and PACF of N_t (Fig. S1A and S1B).

Further details about the times series analysis are presented in Chaves et al. (2012).

2.3. Model and simulations

In this section we briefly explain our model and simulation strategy to re-create the emergence of a 10-week lag correlation between *Ae. aegypti* N_t and TMAX (Fig. 1C).

2.3.1. Model description

Let's assume that an adult mosquito population (N_t) at time t is composed by surviving adults (N_{t-1}) and recruits from emerging larval individuals (J_{t-1} , which is a mathematical abstraction of *Ae. aegypti* aquatic stages, i.e., eggs, larvae and pupae) from the previous time step, $t - 1$, as described by:

$$N_t = sN_{t-1} + pJ_{t-1} \quad (1)$$

where s is the per-capita survival probability of adults and p is the per-capita survival and emergence probability of larvae. Because *A. aegypti* larval developmental time averages approximately a week for the temperatures observed in Thailand when the data was collected (Bar-Zeev, 1958b; Headlee, 1940, 1941; Rueda et al., 1990; Tun-Lin et al., 2000), we can further assume that larvae either emerge as adults, with probability p , or die, with probability $1-p$, after one time step. Experiments and entomological observations suggest that density-dependence regulation of *A. aegypti* (Dye, 1984; Gilpin & McClelland, 1979; Legros et al., 2009; Southwood et al., 1972) occurs primarily during the immature stages. However, *A. aegypti* larval density does not seem to affect adult emergence success when resources are adequate (Bar-Zeev, 1957; Barbosa et al., 1972; Dye, 1982; Wada, 1965) and differences in survival are not significant when comparing low and high resource levels (Rios et al., 1978; Walsh et al., 2011). Nevertheless, emerging individuals are smaller and less fecund on low resources (Bar-Zeev, 1957; Briegel et al., 2002). Assuming that density-dependence can be represented by a function $G(N)$ that describes the regulatory processes acting on the production of larvae (i.e., larvae and eggs) from adults, we have:

$$J_t = G(N_{t-1}) \quad (2)$$

For the density dependence we can employ a phenomenological ‘‘Gompertz’’ exponent θ , whose value is constrained in (0,1), which in addition to a per capita fecundity rate (λ), can be used to define $G(N)$ as follows:

$$J_t = \lambda N_{t-1}^\theta \quad (3)$$

By substituting (3) into (1) we can obtain the following second-order equation:

$$N_t = sN_{t-1} + p(\lambda N_{t-2}^\theta) \quad (4)$$

Alternatively, we can represent (4) as a stage-structured Lefkovich matrix model:

$$\begin{pmatrix} N_t \\ J_t \end{pmatrix} = \begin{pmatrix} s & p \\ \lambda(N_{t-1})^{\theta-1} & 0 \end{pmatrix} \begin{pmatrix} N_{t-1} \\ J_{t-1} \end{pmatrix} \quad (5)$$

The model presented in (5) is unstable at the trivial equilibrium (i.e., mosquito absence; $N^* = 0, J^* = 0$), i.e., once introduced into a new environment mosquitoes will tend to stay. By contrast, at the non-trivial equilibrium: $\left(N^* = \left(\frac{p\lambda}{1-s} \right)^{1/(1-\theta)}; J^* = \lambda \left(\frac{p\lambda}{1-s} \right)^{\theta/(1-\theta)} \right)$, as long as the population is under density-dependent regulation (i.e., $\theta < 1$) the model is stable, i.e., tends to recover to a fixed value following a disturbance (Levins & Wilson, 1980). The model presented in (5) is reactive; i.e., prone to transiently amplify disturbances (Caswell & Neubert, 2005), in other words, a small increase in

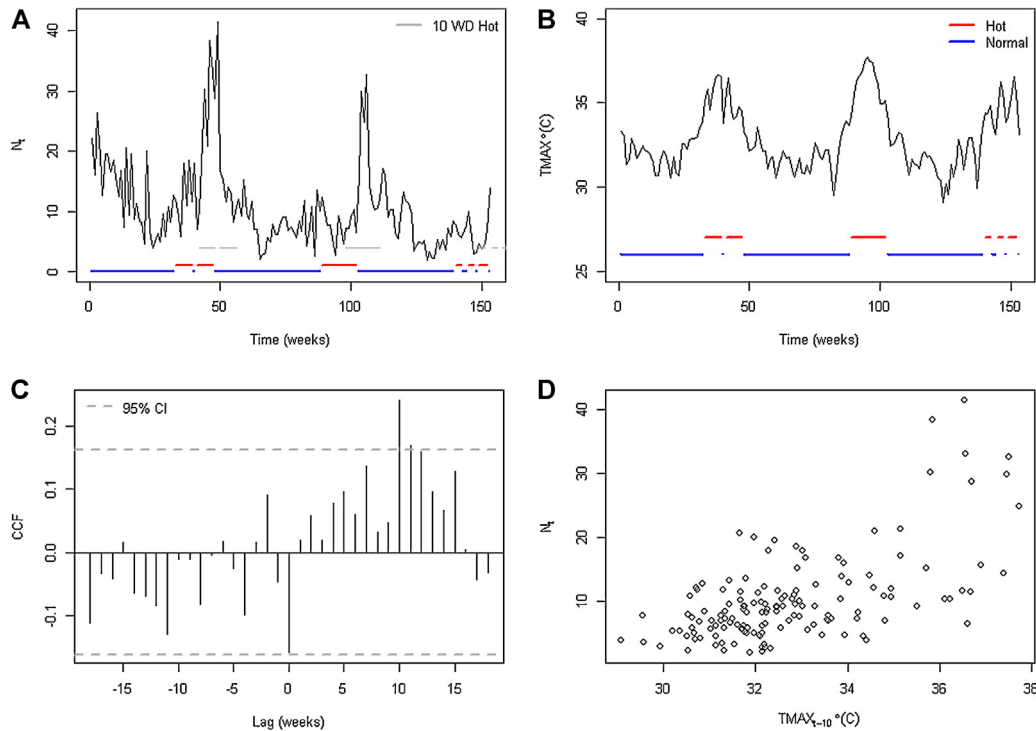


Fig. 1. Data (A) Weekly adult *Aedes aegypti* abundance, N_t , from Village 6, Chachoengsao, Thailand (June 1990–May 1993) (B) Weekly maximum temperature, TMAX ($^\circ\text{C}$), at Chachoengsao, Thailand (June 1990–May 1993) (C) Cross Correlation function (CCF) between pre-whitened residuals of Maximum temperature and a second order autoregressive model of mosquito abundance (D) Weekly adult mosquito abundance, N_t , as function of 10 week lag maximum temperature, TMAX₋₁₀ ($^\circ\text{C}$). In panels (A) and (B) blue and red lines indicate the occurrence of “Normal” ($T \leq 34^\circ\text{C}$) and “Hot” ($T > 34^\circ\text{C}$) environments. In panel (B) the gray line indicates the 10 week delayed “Hot” environment (10 WD Hot). (For interpretation of the references to color in the artwork, the reader is referred to the web version of the article.)

mosquito abundance will grow transiently before the population returns to the equilibrium value expected for the maximum likelihood parameter estimates obtained with the time series described in the Data section (Table S1). For further details on model derivation, sensitivity (i.e., response to changes in parameters), elasticity (i.e., response to proportional changes in parameters), stability and reactivity analyses see Chaves et al. (2012).

2.3.2. Simulation strategy

In the following paragraphs we explain the implementation and evaluation of model simulations. We first define the considered stochastic environments, and then discuss the selection of parameters used for the simulation, the sequential combination of parameters employed to test different hypothesis about demographic parameter change, and finally, the simulation protocol and the evaluation of the simulation results that we performed.

2.3.2.1. Stochastic environments. Fig. 1D shows how mosquito abundance increased with high maximum temperatures (TMAX), especially above 34°C (see also Table S1) suggesting that mosquitoes have alternative strategies for dealing with “normal” ($\text{TMAX} \leq 34^\circ\text{C}$) and “hot” ($\text{TMAX} > 34^\circ\text{C}$) environments. We inspected the maximum temperature time series and determined that 25% of the time the environment was “hot”, while the remaining 75% of the time the environment was “normal”. Autocorrelation (Fig. S1C) and partial autocorrelation (Fig. S1D) functions of TMAX, however, suggest that transitions between the two environments are not-independent, because temperature data is significantly autocorrelated, and indeed the transitions between normal and “hot” environments occur with very heterogeneous probabilities (Table 1). Thus, for the simulation of the stochastic environment we used the acceptance-rejection method (Ross, 1997) to generate environmental sequences of “normal” and

“hot” environments assuming that environments were correlated according to the probabilities presented in Table 1. For comparison we also generated environmental sequences assuming the two environments were independent, occurring with the probability of their frequency on the TMAX time series data.

2.3.2.2. Parameters. In all simulations we employed parameter estimates from various sources. Adult survival (s) and the density-dependence exponent (θ) were estimated from the time series and kept constant in all simulations (Table S1). We also kept these parameters constant for biological reasons. Adult mosquitoes have an increased autonomy from the environment by their flying ability, which allows them to disperse in adverse environments (Edman et al., 1998), probably keeping adult survival (s) constant (Christophers, 1960). Population dynamics are very sensitive to small changes in θ (Chaves et al., 2012), which in principle makes us believe this parameter has low variability, a fact further reinforced by the similarity in estimates from populations as far apart as Puerto Rico and Thailand (Chaves et al., 2012). Based on entomological observations (Bar-Zeev, 1958a; Tun-Lin et al., 2000; Walsh et al., 2011; Wijeyaratne et al., 1974; Yang et al., 2009b) we assumed

Table 1

Frequency and probability of transition between “hot” (average weekly maximum temperature $>34.03^\circ\text{C}$) and normal environments in Village 6, Chachoengsao, Thailand. Conditional probability indicates the probability of changing from environment i to environment j given that environment i is the current environment, i.e., $P(\text{environment } j | \text{environment } i)$ where i and j can be any of the two environments (“hot” or normal).

Environmental transition	Frequency	Probability	Conditional probability
Hot- > Hot	32	0.21	0.84
Hot- > Normal	6	0.04	0.16
Normal- > Hot	6	0.04	0.05
Normal- > Normal	107	0.71	0.95

that high temperatures were detrimental for larvae, decreasing larval survival in the “hot” environment. We assumed larval survival under “normal” environments to be $p_1 = 0.500$ based on field observations (Walsh et al., 2011; Wijeyaratne et al., 1974), an estimate that tends to be smaller than laboratory based estimations (Bar-Zeev, 1958b; Barbosa et al., 1972; Headlee, 1940, 1941; Koenraadt et al., 2010; Tun-Lin et al., 2000). We further assumed that for “hot” environments larval survival was halved, as observed in the laboratory for *Ae aegypti* (Bar-Zeev, 1958a; Mohammed & Chadee, 2011; Rueda et al., 1990; Tun-Lin et al., 2000) and for other culicinae mosquitoes under field conditions (Chaves et al., 2011). Thus, for the “hot” environment we assumed larval survival to be $p_2 = 0.250$. We also assumed the transition from normal to “hot” environments could further decrease survival ($p_3 < p_2$) based on observations from experiments where *Ae aegypti* larval mortality increased and then decreased following environmental disturbances (Agudelo-Silva & Spielman, 1984; Wilson et al., 1990). Using the estimate for the product of larval survival and fecundity ($\bar{\lambda}p$, Table S1) we were able to estimate the fecundity for normal ($\lambda_1 = 3.42$) and “hot” ($\lambda_2 = 6.84$) environments under the assumption of a fecundity-survival trade-off (Stearns, 2000), which is a plausible assumption for *Ae aegypti* (Wong et al., 2012). The fecundity-survival trade-off assumes the product of fecundity and larval survival to be constant ($\lambda_1 p_1 = \lambda_2 p_2 = \bar{\lambda}p$). We further assumed that fecundity might increase in an over-compensatory mode; i.e., increasing the size of the adult mosquito population at equilibrium (by adding the estimated impact of the forcing, Exo , to the population size at equilibrium, N^* , i.e., $N^* + Exo$) and solving the following equation:

$$N^* + Exo = s(N^*) + p_2 \lambda_3 (N^*)^\theta \tag{6}$$

for λ_3 . Taking the average estimated forcing for the “hot” environments ($\bar{Exo} = 3.6$) we estimated the following overcompensated fecundity ($\lambda_3 = 8.48$). In a set of simulations we also assumed the presence of further environmental noise, which is defined as perturbations affecting all individuals in a population at a given time (Mangel, 2006). Under this assumption, the right hand side of equations (4) is log-transformed (Dennis & Taper, 1994), and the resulting left hand side of the equation, z_t , is assumed to be normal, i.e., $z_t \sim N(\log(N_t), \sigma_{envs}^2)$, where $\sigma_{envs}^2 = 0.181$ was estimated from the time series (Table S1). Table 2 shows the parameters we employed in the simulations.

2.3.2.3. Sequential demographic parameter changes for transitions between normal and “hot” environments. The transition probability from “normal” to “hot” environments renders the estimation of an average timespan for “hot” environments, which can be assumed to have a geometric distribution. The environmental change from “hot” back to normal can be seen as the time to the first failure in a series of Bernoulli trials (Mangel, 2006). From Table 1, it can be estimated that on average a hot environment should last around 6 weeks (i.e., 1/probability of changing to normal given the environment is “hot”). With this information we defined 8 sequences

Table 2
Parameters employed in the simulations.

Parameter	Estimate	Source
Adult survival (s)	0.317	Chaves et al. (2012)
Denso-dependence exponent (θ)	0.505	Chaves et al. (2012)
Larval survival (p)	$p_1 = 0.5$ $p_2 = 0.25$ $p_3 < p_2$	Walsh et al. (2011), Wijeyaratne et al. (1974)
Fecundity (λ)	$\lambda_1 = 3.42$ $\lambda_2 = 6.84$ $\lambda_3 = 8.48$	Chaves et al. (2012) ^a
Variance of the environmental noise (σ_{envs}^2)	0.181	Chaves et al. (2012)

^a Assuming a trade off with larval survival ($\lambda_1 p_1 = \lambda_2 p_2$) or an over-compensatory fecundity following a hot environment ($\lambda_3 > \lambda_2$), see Section 2.3.2.2 for further details.

of larval survival (p) and fecundity (λ) changes shorter than 6 weeks (Table 3) to test each sequence ability to generate a 10 week delayed association between TMAX and mosquito population size. Briefly, case 1 and 2 are controls where the transition from a “normal” to “hot” environment decreases p and increases λ to compensate (case 1) or over-compensate (case 2) the change in p . In case 3 following the transition to a “hot” environment p decreased and after one week λ increased in a compensatory manner. Case 4 is similar to 3 but after the transition to a normal environment the increased fecundity of the hot environment last 1 week. Case 5 is similar to case 4, but after the compensation in the “hot” environment λ further increases to over-compensatory. In case 6 p decreases following the transition to a “hot” environment, but then increases (to a value below the one for the “normal” environment) together with λ which also becomes over-compensatory. Finally, cases 7 and 8 consider a two-step change in p (larval survival decreases and then recovers, yet is smaller than before the advent of the hot environment) and also in λ (fecundity compensates for the change in survival before increasing to an over-compensatory level). In case 8 over-compensatory λ spans two weeks once the environment is back to “normal”.

2.3.2.4. Simulation protocol. For each one of the cases in Table 3 we generated 1000 replications of random environments that were 1200 week long. Each replicate was used to iterate equation (4), where the initial conditions were the estimated larval and adult population at the non-trivial equilibrium of Eq. (4); i.e., when $N^* \neq 0$, for the parameters presented in Table S1, and parameters for a given environment changed according to the rules defined in Table 3. We keep the last 180 values of population size and the environment and computed the cross correlation function between these two variables for 19 lags (lag -19 to +19). We also computed the mean, maximum, 25th and 75th quantiles, variance, skewness and kurtosis of the simulated mosquito abundance time series, as well as the average environment using scores presented in Table 3. We also performed this protocol assuming the presence

Table 3
Larval survival (p_i) and fecundity (λ_i) for transitions between normal and “hot” environments. The following relationships between parameters were considered: $\lambda_1 p_1 = \lambda_2 p_2$; $\lambda_3 > \lambda_2 > \lambda_1$; $p_1 > p_2 > p_3$. The values inside () in each case indicate the score employed to estimate the value of the average environment. Scores are based on ranking the values of $\lambda_i p_i$, and solving ties based of the value of λ_i for $i \in \{1, 2, 3\}$. In cases 5–8 the exogenous forcing is included through an over-compensatory fecundity (λ_3).

Environment	Normal	Hot	Hot	Hot	Hot	...	Hot	Normal	Normal
Control A (case 1)	$\lambda_1, p_1(3)$	$\lambda_2, p_2(4)$	$\lambda_2, p_2(4)$	$\lambda_2, p_2(4)$	$\lambda_2, p_2(4)$...	$\lambda_2, p_2(4)$	$\lambda_1, p_1(3)$	$\lambda_1, p_1(3)$
Control B (case 2)	$\lambda_1, p_1(3)$	$\lambda_3, p_2(4)$	$\lambda_3, p_2(4)$	$\lambda_3, p_2(4)$	$\lambda_3, p_2(4)$...	$\lambda_3, p_2(4)$	$\lambda_1, p_1(3)$	$\lambda_1, p_1(3)$
Case 3	$\lambda_1, p_1(3)$	$\lambda_1, p_2(2)$	$\lambda_2, p_2(4)$	$\lambda_2, p_2(4)$	$\lambda_2, p_2(4)$...	$\lambda_2, p_2(4)$	$\lambda_1, p_1(3)$	$\lambda_1, p_1(3)$
Case 4	$\lambda_1, p_1(3)$	$\lambda_1, p_2(2)$	$\lambda_2, p_2(4)$	$\lambda_2, p_2(4)$	$\lambda_2, p_2(4)$...	$\lambda_2, p_2(4)$	$\lambda_2, p_1(5)$	$\lambda_1, p_1(3)$
Case 5	$\lambda_1, p_1(3)$	$\lambda_1, p_2(2)$	$\lambda_2, p_2(4)$	$\lambda_3, p_2(5)$	$\lambda_3, p_2(5)$...	$\lambda_3, p_2(5)$	$\lambda_3, p_1(6)$	$\lambda_1, p_1(3)$
Case 6	$\lambda_1, p_1(3)$	$\lambda_1, p_3(2)$	$\lambda_3, p_2(4)$	$\lambda_3, p_2(4)$	$\lambda_3, p_2(4)$...	$\lambda_3, p_2(4)$	$\lambda_3, p_1(5)$	$\lambda_1, p_1(3)$
Case 7	$\lambda_1, p_1(3)$	$\lambda_1, p_3(1)$	$\lambda_2, p_3(4)$	$\lambda_2, p_2(4)$	$\lambda_3, p_2(5)$...	$\lambda_3, p_2(5)$	$\lambda_3, p_1(6)$	$\lambda_1, p_1(3)$
Case 8	$\lambda_1, p_1(3)$	$\lambda_1, p_3(1)$	$\lambda_2, p_3(4)$	$\lambda_2, p_2(4)$	$\lambda_3, p_2(5)$...	$\lambda_3, p_2(5)$	$\lambda_3, p_1(6)$	$\lambda_3, p_1(6)$

of environmental noise and for Case 2 assuming an independent environment (see Section 2.3.2.1)

2.3.2.5. Evaluation of the simulation results. The output of the simulations was evaluated in two phases. First, we evaluated the ability of the model (following the sequences of Table 3 for “hot” environments) to generate cross correlation functions between mosquito abundance and TMAX resembling the pattern observed in Village 6, Chachoengsao, Thailand, i.e., with TMAX leading mosquito abundance by 10 weeks (Fig. 1C). For this goal we computed the probability of 19 lags to have the maximum cross correlation for each case in Table 3. We counted the frequency of each lag having the maximum cross-correlation and divided these counts by the number of replications for each case (i.e., 1000) to obtain the probability of a maximum cross correlation for each lag. With this information we determined the best sequence of changes in p and λ as the one with the highest probability to generate the 10 week lag association between TMAX and mosquito abundance. Second, we evaluated the performance of the model to recreate the average, 25th and 75th quantile & maximum, as well as the variance and higher order moments of variability (skewness and kurtosis) of mosquito population size recorded in the field data from Thailand. For these parameters, we determined whether estimates from the Thai time series were contained within the 95% non-extreme estimates from the simulations (i.e., within the 2.5 and 97.5 quantiles of the empirical distributions from simulation estimates).

3. Results

Fig. 2 shows the results from simulations assuming independent and autocorrelated environments. Fig. 2A shows that independent environments invariably lead to a 2 week lag maximum cross

correlation between TMAX and N_t . For the autocorrelated environment (Fig. 2B) the lag for the maximum CCF between TMAX and N_t occurs between 1 and 3 weeks. The addition of environmental noise leads to a 1 week lag maximum cross correlation between TMAX and N_t in an independent environment (Fig. 2C). Environmental noise also generates a distribution where the probability of 0 week lag becomes maximum in the autocorrelated environment (Fig. 2D). Environmental noise in an autocorrelated environment generates a probability distribution where association between mosquito abundance and TMAX for lags of 4 weeks or more (Fig. 2D) is more likely to occur than when noise is present in independent environments (Fig. 2C). Here, it is important to highlight that in Fig. 2 probability for negative, $-$, lag correlation and 12+ are cumulative for several lags. Thus, this preliminary comparison between independent and autocorrelated environments suggests that autocorrelated environments can delay the lag of the association between TMAX and N_t .

Fig. 3 shows the result for the sequence of changes in demographic parameters that maximized the probability of a 10 week lag maximum CCF, which was case 6 of Table 3. In general the probability of 10 week lag having the maximum CCF was very low, slightly above 2% in the best cases, being maximal for $p_3 = 0.10$ (Fig. 3A). For the case of $p_3 = 0.10$ the maximum CCF occurred at 5 weeks of lag (Fig. 3B). It is worth noticing that maximum CCF at 5 weeks of lag was independent of p_3 (Fig. 3C). However, the correlation at 10 week of lag emerged only when environmental noise was considered, being maximized when $p_2 > p_3$, and maximized for higher lags when $p_3 = 0.10$ (Fig. 3D). Interestingly case 6 of Table 3 had the highest probability to produce the longest delays for the maximum CCF, both assuming stochastic environments (for comparison with other cases see Fig. S2) and stochastic environments with environmental noise (for comparison with other cases see Fig. S3).

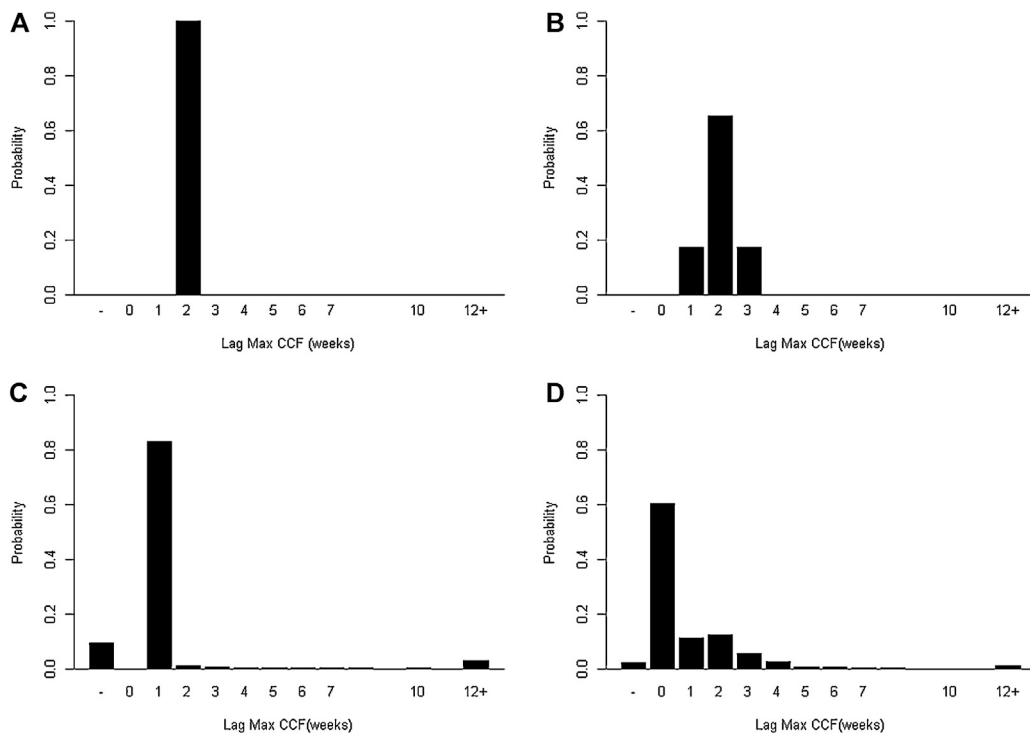


Fig. 2. Probability for maximum cross correlation lags (Lag Max CCF) between the environment and *Aedes aegypti* abundance for simulations assuming: (A) an autonomous, time independent stochastic environment (B) a non-autonomous autocorrelated stochastic environment (C) an autonomous, time independent stochastic environment and multiplicative environmental noise (D) a non-autonomous autocorrelated stochastic environment and multiplicative environmental noise. In all the simulations we employed the parameters presented in Table S1, with the exception of fecundity (λ) and larval survival (p) in “hot” environments, which were changed to ($\lambda = 8.48$, $p = 0.25$). In the x axis of all panels “-” denotes all negative lags and “12+” lag 12 and higher. (B) and (D) correspond to control II (case 2) of Table 3.

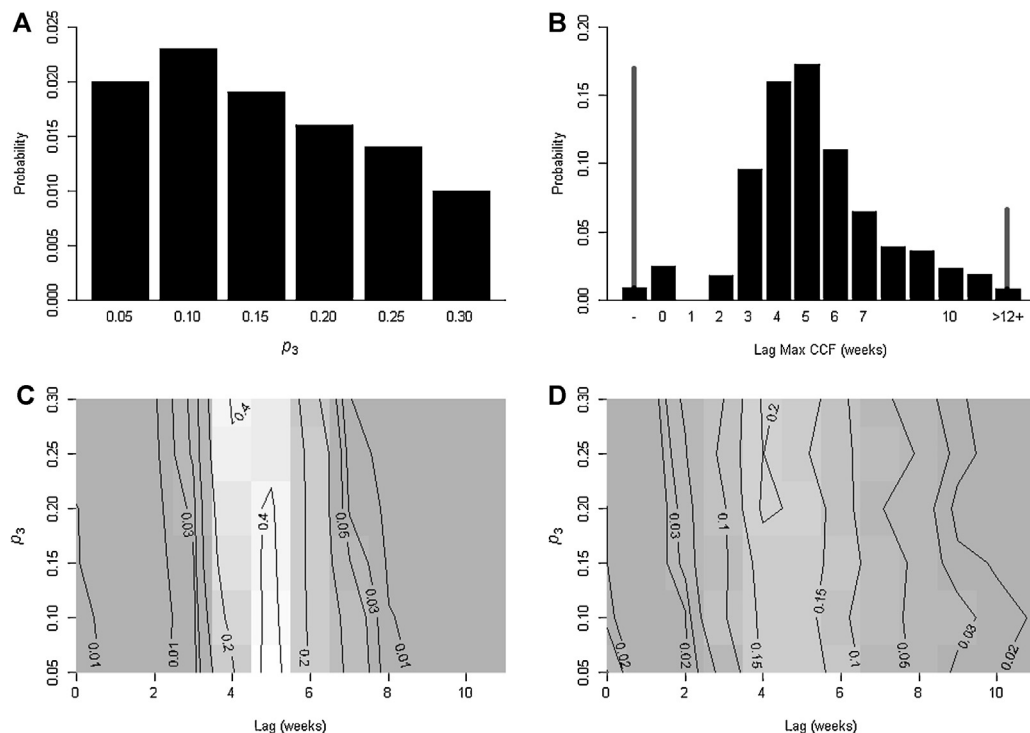


Fig. 3. Model simulation summary from the best life history parameter transition sequence able to explain the maximum temperature and *Aedes aegypti* adult abundance cross-correlation patterns observed at Village 6, Chachoengsao, Thailand (A) Probability of lag 10 weeks having the maximum cross correlation between mosquito abundance and maximum temperature as function of larval survival probability (p) following a “normal” to “hot” environmental transition (B) Probability for maximum cross correlation lags (Lag Max CCF) from simulations assuming a non-autonomous autocorrelated environment and multiplicative environmental noise. In the x axis of this panel “-” denotes all negative lags and “>12+” lag 12 and higher. At “-” and “>12+” gray lines indicate cumulative probability and black bars the average probability, respectively, for any negative lag and 12 and higher lags (C) Probability contour of maximum cross correlation lags (Lag Max CCF) as function of larval survival probability (p) obtained from simulations assuming a non-autonomous autocorrelated stochastic environment (D) Probability contour of maximum cross correlation lags (Lag Max CCF) as function of larval survival probability (p) obtained from simulations assuming a non-autonomous autocorrelated environment and multiplicative environmental noise. In (C) and (D) a darker gray tone indicates a lower correlation. For reference, the best life history parameter transition sequence is case 6 in Table 3.

Fig. 4 shows a detailed evaluation of simulation results from case 6 (Table 3) assuming a stochastic and autocorrelated environment with environmental noise. Fig. 4A presents the distribution of the observations from Thailand, which shows the abundance to be positively skewed with frequent mosquito outbreaks. Fig. 4(B–H) show the distribution of the simulation outputs for the mean (Fig. 4B), maxima (Fig. 4C), 25th (Fig. 4D) and 75th (Fig. 4E) quantiles, variance (Fig. 4F), skewness (Fig. 4G) and kurtosis (Fig. 4H). In all cases the observed values from the original time series were inside the 95% non-extreme outputs of the simulations (i.e., within the 2.5 and 97.5 quantiles of the empirical distributions from simulation estimates), indicating the success of the model not only to generate the 10 week delayed maximum CCF between TMAX and N_t , but also the different moments and 25th and 75th quantiles of the observed distribution at Village 6, Chachoengsao, Thailand. Fig. 4I shows the size of the 75th quantile of the simulations distribution as function of the average environment, showing a linear increase of this quantile [a proxy measurement of mosquito outbreaks] with the average environment.

In summary, our results showed that autocorrelated stochastic environments, environmental noise and sequential changes in demographic parameters could generate a 10 week delay in the association between increased temperatures and mosquito outbreaks, a pattern observed in Thailand (Fig. 1). Delays emerged following sequential changes in demographic parameters after the onset of “hot” environments, specifically: (1) a decreased larvae survival; (2) an over-compensatory fecundity increase that lasts until the environment returns to “normal”; (3) a larvae survival increase when the environment returns to “normal”, (3)

a fecundity decrease to its original value following the increase in larval survival once in the “normal” environment.

4. Discussion

4.1. Hot environments and mosquito outbreaks

Sudden extraordinary changes in species abundance (i.e., outbreaks), have been mostly studied in insects, primarily agricultural pests (Berryman & Stark, 1985), but also medically important species, especially mosquitoes (Chase & Knight, 2003; Yang et al., 2009a). In fact, it could be argued that insect outbreaks have underpinned the wider ecological discussion on whether populations undergo density dependent-regulation (Chaves & Koenraadt, 2010; Nicholson, 1958). In the applied context of disease control, vector outbreaks are of major importance given density-dependence implications for different control measures, such as larviciding (Agudelo-Silva & Spielman, 1984; Wilson et al., 1990), insecticide spraying (Newton & Reiter, 1992; Oki et al., 2011), and more recently, the field release of genetically modified mosquitoes (Legros et al., 2009; Magori et al., 2009).

Here, we tried to understand the association between extreme weather and mosquito outbreaks in a population with clear signatures of density-dependence (Chaves et al., 2012; Dye, 1984; Southwood et al., 1972). Our previous analysis showed that extreme “hot” temperatures (above 34 °C) were associated with delayed outbreaks of *Ae. aegypti*, in a very localized fashion, yet our study did not fully explain the emergence of a 10 week delay in the association between extreme “hot” temperatures and unusually

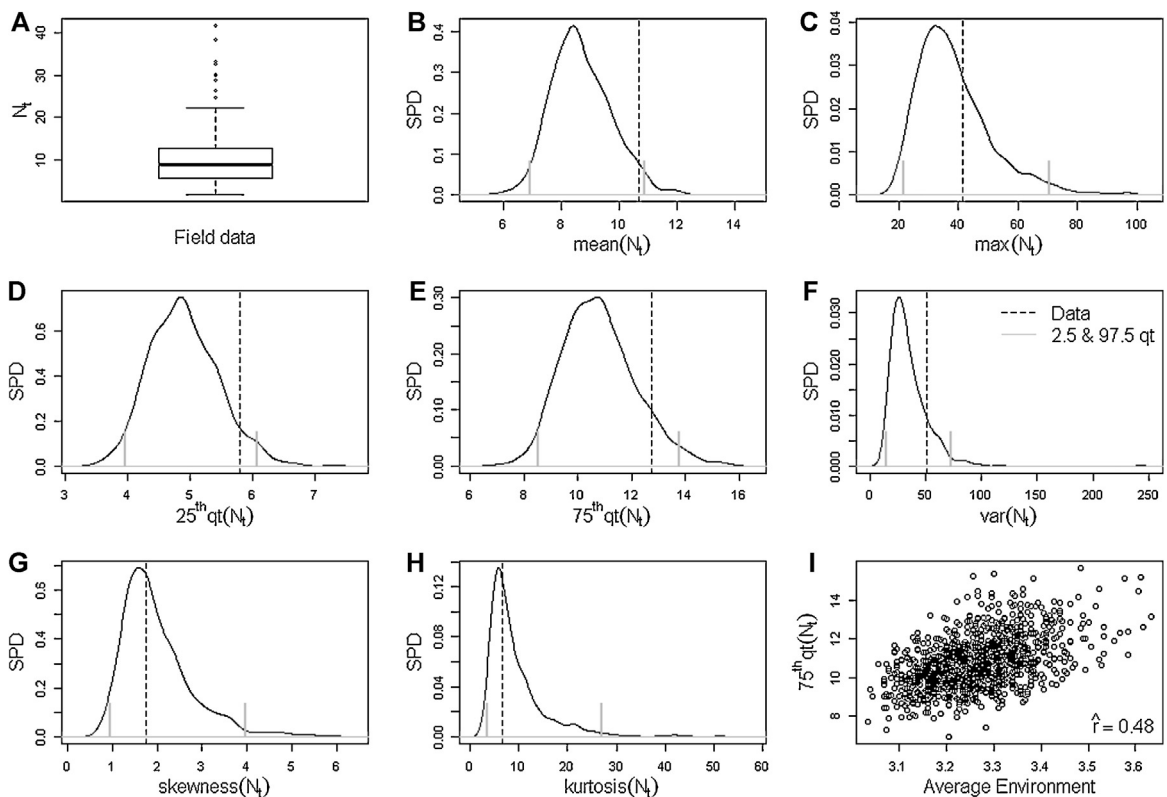


Fig. 4. Evaluation of model simulations (A) Boxplot of the Village 6, Chachoengsao, Thailand adult *Aedes aegypti* abundance, N_t , time series. The middle bar indicates the median of the distribution and the box the 25th and 75th quantiles (qt) of the distribution. (B) Smoothed probability density (SPD) of the mean N_t . In this and subsequent panels gray bars indicate the 5% most extreme simulations (2.5% to the left and right of the distribution) and the black dashed line is the estimate from the time series (C) SPD of the maximum N_t (D) SPD of N_t 25th quantile (E) SPD of N_t 75th quantile (F) SPD of N_t variance (G) SPD of N_t skewness (H) SPD of N_t kurtosis (I) N_t 75th quantile as function of the average environment.

large mosquito abundance (Chaves et al., 2012). In our previous study we accounted for this localized association between extreme temperatures and mosquito outbreaks by adding a non-linear function of temperature to a density-dependent delayed recruitment model. Nevertheless, as clearly noted by Schmalhausen (1949) and Levins (1968) the impacts of the changing environments are canalized by the individuals, i.e., demographic parameters are likely to change in order to ensure population persistence in a different environment (Tuljapurkar, 1985, 1989). In the case of rainfall, association delays tend to be shorter, between 1 and 4 weeks (Barrera et al., 2011; Scott et al., 2000) and it can be argued that changes in adult recruitment by rainfall induced generation of larval habitats could underlie the outbreaks (Chase & Knight, 2003; Chaves et al., 2012; Yang et al., 2009a). In this sense, rainfall and associated changes in relative humidity could ease mosquito dispersal (Edman et al., 1998) which maybe essential for population persistence even if local mosquito larval sources are not viable, as suggested by metapopulation persistence of locally inviable populations in models that consider dispersal in autocorrelated environments (Roy et al., 2005). By contrast, hot temperatures are known to increase larval mortality in *Ae. aegypti* (Bar-Zeev, 1958a; Mohammed & Chadee, 2011), as well as other mosquitoes (Chaves et al., 2011). These observations imply that a series of compensatory or over-compensatory changes in life history traits (e.g., fecundity compensating changes in survival) could be expected if mosquito life history is governed by fitness trade-offs (Stearns, 2000). In that sense our model simulations suggest that an increase in temperature could be linked with both a decrease in larval survival and an over-compensatory increase in fecundity, a result indirectly suggested by the potential fitness increase of emerging *Ae. aegypti* adults from larvae subjected to external

mortality (Wilson et al., 1990). We also found the correlated structure of the environment to be important for the generation of delayed mosquito outbreaks. A model under the assumption of independent environmental transitions was unable to re-create the delay between extreme hot temperatures and mosquito outbreaks. Moreover, the assumption of environmental independence is likely wrong because both the ACF and PACF of TMAX indicate that TMAX has an auto-correlated nature (Fig. S1C and S1D).

Our model simulations also suggest the emergence of delayed outbreaks to be linked with sequential changes in demographic parameters following the onset of “hot” environments. This result has implications for entomological and modeling research. Previous studies have shown that mosquitoes do change their phenotypes following environmental fluctuations. For example, changes have been observed in body size, which tends to be larger at low temperatures (Scott et al., 2000; Tsuda & Takagi, 2001). Mosquito body size is positively associated with fecundity (Bar-Zeev, 1957), male sperm quality (Ponlawat & Harrington, 2007), survival (Tsuda & Takagi, 2001) and overall fitness (Koenraadt, 2008), a pattern shared by other mosquito species (Reisen et al., 1984). How these changes correlate with a given population demographic parameters or if they are progressive after the onset of relatively stable environmental conditions is an open question (Stearns, 1981). We also want to emphasize that our results likely derive from specific sequential changes in life history traits, because for the same fixed parameters the delayed pattern only emerged with a given sequence of changes, in parameters whose proportional changes have relative little impact on the dynamics as revealed by a perturbation (i.e., parameter sensitivity and elasticity) analysis we performed in our previous study of this model (Chaves et al., 2012). In that sense, parameter estimates from

different environmental conditions, based on semi-natural experiments in heterogeneous and fluctuating environments (Carrington et al., 2013; Chaves et al., 2011), would help to better understand the impacts of temperature on larval survival and the associated changes or trade-offs with fecundity (Stearns, 2000). Ultimately, this entomological research could provide a basis to test the existence of sequential changes in life history traits with the advent of “hot” environments, a phenomenon that is becoming increasingly more frequent worldwide (Hansen et al., 2012; Rahmstorf & Coumou, 2011). From the modeling perspective, analytical results for population growth in autocorrelated environments (Tuljapurkar, 1982) need to be extended to non-linear (density-dependent) cases or generalized for non-Markovian situations (where memory goes beyond the previous time step in discrete time models).

A detailed dissection of delays in the association between extreme high temperatures and mosquito outbreaks in light of ecological theory suggest that they could emerge by the joint action of several factors. First, as originally noticed by Dye (1984) the delayed recruitment of adults can lead to generational cycles (May et al., 1974). Although our model also considers delayed adult recruitment (Chaves et al., 2012), this feature alone cannot explain mosquito outbreaks, nor the localized nature of the association between high temperatures and the outbreaks. Moreover, generational delays often do not destabilize equilibria in stage-structured models (Rodríguez, 1998), and our model is numerically stable for the parameters we employed in the simulations, and structurally stable when density-dependence exists, i.e., $\theta < 1$ (Chaves et al., 2012). Nevertheless, our model is reactive, thus able to transiently amplify perturbations and generate the autocorrelation patterns we observed in the mosquito abundance time series data (Chaves et al., 2012). The introduction of sequential and over-compensatory changes in the life history of *Ae aegypti* could lengthen the delay of the association beyond what can be attributed to a reactive response, with an average of 4–5 weeks (Fig. 3C and D). These environmentally forced “cycles” can then be amplified if they coincide with reactive response in the model, a result independently derived for matrix models (Costantino et al., 1998; Tuljapurkar, 1985) and ordinary differential equations (Nisbet & Gurney, 1976). In fact, the 5 week cycles can resonate and generate association delays of sub-harmonic length (i.e., a multiple of 4 or 5 weeks), for example 10 weeks. In our simulations, however, resonance alone by the stochastic environment could only lengthen the association delay to 8 weeks, with the emergence of 10 week delay association only observed when additional environmental noise was considered. In fact, the additional environmental noise can be amplified by the reactive nature of the model (Verdy & Caswell, 2008). The nature of the additional environmental noise could be related to other environmental factors. For example, mosquito wing size was primarily correlated with relative humidity (Morales Vargas et al., 2010), indicating that beyond temperature, mosquito development and body size could be sensitive to many factors.

4.2. Implications for control

Our results suggest that more variable temperature regimes and extended “hot” environments could be associated with increased mosquito outbreaks. This feature is common to other insects, where variable environments can lead to larger average population size when compared with stable environments (Costantino et al., 1998). In that sense, forecasts concerning unusual temperature increases could help to temporally target interventions of highly productive larval developmental containers (Maciel-de-Freitas & Lourenco-de-Oliveira, 2011) and other refugia that potentially promote mosquito outbreaks (Wallner, 1987). The advent of “hot” environments is a time when interventions can be

highly successful in diminishing the entomological risk of disease transmission by *Ae aegypti*. Nevertheless, a challenge is that such times can be associated with decreased interest on implementing an intervention given the high likelihood of decreased mosquito abundance and nuisance (Predescu et al., 2006).

4.3. Synthesis

Model simulations showed that mosquito outbreaks are likely the product of reactive population dynamics and over-compensatory fecundity following increased larval mortality in auto-correlated environments. In more variable environments, where transitions to the “hot” environment are more prevalent, we can expect an increased occurrence of *Ae aegypti* outbreaks. Control strategies could benefit from targeting highly productive mosquito refugia during “hot” periods even if mosquito abundance is nil, especially because a temperature shift might signal upcoming outbreak. Control interventions at these times, even if counterintuitive given the likely low mosquito density, could decrease *Ae aegypti* population expansion and its associated entomological risk for increased pathogen transmission.

Acknowledgements

This research was funded by Nagasaki University (Program for Nurturing Global Leaders in Tropical and Emerging Communicable Diseases and Cooperative Grant) and Japan Society for the Promotion of Science. This work also benefited from discussions with working group members in the Research and Policy for Infectious Disease Dynamics (RAPIDD) program of the Science and Technology Directorate, Department of Homeland Security, and the Fogarty International Center, National Institutes of Health, USA. LFC and TT wish to dedicate this article to the memory of their friend Shoichi Yamada, who left too early.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.actatropica.2013.02.025>.

References

- Agudelo-Silva, F., Spielman, A., 1984. Paradoxical effects of simulated larviciding on production of adult mosquitos. *Am. J. Trop. Med. Hyg.* 33, 1267–1269.
- Bar-Zeev, M., 1957. The effect of density on the larvae of a mosquito and its influence on fecundity. *Bull. Res. Council. Isr. Sect. B* 6, 220–228.
- Bar-Zeev, M., 1958a. The effect of extreme temperatures on different stages of *Aedes aegypti* (L.). *Bull. Entomol. Res.* 48, 593–599.
- Bar-Zeev, M., 1958b. The effect of temperature on the growth rate and survival of the immature stages of *Aedes aegypti* (L.). *Bull. Entomol. Res.* 49, 157–163.
- Barbosa, P., Peters, T.M., Greenough, N.C., 1972. Overcrowding of mosquito populations: responses of larval *Aedes aegypti* to stress. *Environ. Entomol.* 1, 89–93.
- Barker, C.M., Eldridge, B.F., Reisen, W.K., 2010. Seasonal abundance of *Culex tarsalis* and *Culex pipiens* complex mosquitoes (Diptera: Culicidae) in California. *J. Med. Entomol.* 47, 759–768.
- Barrera, R., Amador, M., MacKay, A.J., 2011. Population dynamics of *Aedes aegypti* and dengue as influenced by weather and human behavior in San Juan, Puerto Rico. *PLoS Negl. Trop. Dis.* 5, e1378.
- Barrera, R., Avila, J., Gonzalez-Tellez, S., 1993. Unreliable supply of potable water and elevated *Aedes aegypti* larval indices – a casual relationship. *J. Am. Mosq. Control Assoc.* 9, 189–195.
- Berryman, A.A., Stark, R.W., 1985. Assessing the risk of forest insect outbreaks. *Z. für Angew. Entomol.* 99, 199–208.
- Briegel, H., Hefti, M., DiMarco, E., 2002. Lipid metabolism during sequential gonotrophic cycles in large and small female *Aedes aegypti*. *J. Insect Physiol.* 48, 547–554.
- Carrington, L.B., Seifert, S.N., Willits, N.H., Lambrechts, L., Scott, T.W., 2013. Large diurnal temperature fluctuations negatively influence *Aedes aegypti* (Diptera: Culicidae) life-history traits. *J. Med. Entomol.* 50, 43–51.
- Caswell, H., Neubert, M.G., 2005. Reactivity and transient dynamics of discrete-time ecological systems. *J. Differ. Equ. Appl.* 11, 295–310.

- Chase, J.M., Knight, T.M., 2003. Drought-induced mosquito outbreaks in wetlands. *Ecol. Lett.* 6, 1017–1024.
- Chaves, L.F., Keogh, C.L., Nguyen, A.M., Decker, G.M., Vazquez-Prokopec, G.M., Kitron, U.D., 2011. Combined sewage overflow accelerates immature development and increases body size in the urban mosquito *Culex quinquefasciatus*. *J. Appl. Entomol.* 135, 611–620.
- Chaves, L.F., Koenraad, C.J.M., 2010. Climate change and highland malaria: fresh air for a hot debate. *Q. Rev. Biol.* 85, 27–55.
- Chaves, L.F., Morrison, A.C., Kitron, U.D., Scott, T.W., 2012. Nonlinear impacts of climatic variability on the density-dependent regulation of an insect vector of disease. *Glob. Change Biol.* 18, 457–468.
- Christophers, S.R., 1960. *Aedes aegypti* (L) the Yellow Fever Mosquito: its Life History, Bionomics and Structure. Cambridge University Press, Cambridge.
- Costantino, R.F., Cushing, J.M., Dennis, B., Desharnais, R.A., Henson, S.M., 1998. Resonant population cycles in temporally fluctuating habitats. *Bull. Math. Biol.* 60, 247–273.
- Dennis, B., Taper, M.L., 1994. Density dependence in time series observations of natural populations: estimation and testing. *Ecol. Monogr.* 64, 205–224.
- Dibo, M.R., Chierotti, A.P., Ferrari, M.S., Mendonça, A.L., Chiaravalloti Neto, F., 2008. Study of the relationship between *Aedes (Stegomyia) aegypti* egg and adult densities, dengue fever and climate in Mirassol, state of São Paulo, Brazil. *Mem. I. Oswaldo Cruz.* 103, 554–560.
- Dye, C., 1982. Intraspecific competition amongst larval *Aedes aegypti* – food exploitation or chemical interference. *Ecol. Entomol.* 7, 39–46.
- Dye, C., 1984. Models for the population dynamics of the yellow fever mosquito, *Aedes aegypti*. *J. Anim. Ecol.* 53, 247–268.
- Edman, J.D., Scott, T.W., Costero, A., Morrison, A.C., Harrington, L.C., Clark, G.G., 1998. *Aedes aegypti* (Diptera: Culicidae) movement influenced by availability of oviposition sites. *J. Med. Entomol.* 35, 578–583.
- Foo, L.C., Kim, T.W., Lee, H.L., Fang, R., 1985. Rainfall, abundance of *Aedes aegypti* and dengue infection in Selangor, Malaysia. *South East Asian J. Trop. Med. Public Health* 16, 560–568.
- Gilpin, M.E., McClelland, G.A.H., 1979. Systems-analysis of the yellow-fever mosquito *Aedes aegypti*. *Fortschr. Zool.* 25, 355–388.
- Gubler, D.J., 1989. *Aedes aegypti* and *Aedes aegypti*-borne disease control in the 1990s: top down or bottom up. *Am. J. Trop. Med. Hyg.* 40, 571–578.
- Hansen, J., Sato, M., Ruedy, R., 2012. Perception of climate change. In: *Proceedings of the National Academy of Sciences*.
- Harrington, L.C., Edman, J.D., Scott, T.W., 2001. Why do female *Aedes aegypti* (Diptera: Culicidae) feed preferentially and frequently on human blood? *J. Med. Entomol.* 38, 411–422.
- Hayes, J., Downs, T.D., 1980. Seasonal changes in an isolated population of *Culex pipiens quinquefasciatus* (Diptera: Culicidae): a time series analysis. *J. Med. Entomol.* 17, 63–69.
- Headlee, T.J., 1940. The relative effects on insect metabolism of temperatures derived from constant and variable sources. *J. Econ. Entomol.* 33, 361–364.
- Headlee, T.J., 1941. Further studies of the relative effects on insect metabolism of temperatures derived from constant and variable sources. *J. Econ. Entomol.* 34, 171–174.
- Ho, B.C., Chan, K.L., Chan, Y.C., 1971. *Aedes aegypti* (L.) and *Aedes albopictus* (Skuse) in Singapore city 3. Population fluctuations. *Bull. World Health Organ.* 44, 635–640.
- Koenraad, C.J.M., 2008. Pupal dimensions as predictors of adult size in fitness studies of *Aedes aegypti* (Diptera: Culicidae). *J. Med. Entomol.* 45, 331–336.
- Koenraad, C.J.M., Kormaksson, M., Harrington, L.C., 2010. Effects of inbreeding and genetic modification on *Aedes aegypti* larval competition and adult energy reserves. *Parasit. Vectors* 3, 92.
- Legros, M., Lloyd, A.L., Huang, Y.X., Gould, F., 2009. Density-dependent intraspecific competition in the larval stage of *Aedes aegypti* (Diptera: Culicidae): revisiting the current paradigm. *J. Med. Entomol.* 46, 409–419.
- Levins, R., 1968. *Evolution in Changing Environments. Some Theoretical Explorations*. Princeton University Press, Princeton.
- Levins, R., Wilson, M., 1980. *Ecological theory and pest-management*. *Annu. Rev. Entomol.* 25, 287–308.
- Maciel-de-Freitas, R., Lourenço-de-Oliveira, R., 2011. Does targeting key-containers effectively reduce *Aedes aegypti* population density? *Trop. Med. Int. Health* 16, 965–973.
- Magori, K., Legros, M., Puente, M.E., Focks, D.A., Scott, T.W., Lloyd, A.L., Gould, F., 2009. Skeeeter buster: a stochastic, spatially explicit modeling tool for studying *Aedes aegypti* population replacement and population suppression strategies. *PLoS Negl. Trop. Dis.* 3, e508.
- Makiya, K., 1973. Population dynamics of mosquitoes in Nagoya district V. Seasonal change of composition rate of *Culex pipiens molestus* and *Culex pipiens pallens* observed in a midtown building. *Jpn. J. Sanitary Zool.* 24, 89–96.
- Makiya, K., 1974. Population dynamics of mosquitoes in Nagoya district B. Larval and imaginal populations of *Aedes albopictus* (Skuse) in a cemetery of Nagoya City. *Jpn. J. Sanitary Zool.* 25, 41–49.
- Mangel, M., 2006. *The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology*. Cambridge University Press, Cambridge.
- May, R.M., Conway, G.R., Hassell, M.P., Southwood, Tr., 1974. Time delays, density-dependence and single-species oscillations. *J. Anim. Ecol.* 43, 747–770.
- Minakawa, N., Sonye, G., Mogi, M., Githeko, A., Yan, G.Y., 2002. The effects of climatic factors on the distribution and abundance of malaria vectors in Kenya. *J. Med. Entomol.* 39, 833–841.
- Mohammed, A., Chadee, D.D., 2011. Effects of different temperature regimens on the development of *Aedes aegypti* (L.) (Diptera: Culicidae) mosquitoes. *Acta Trop.* 119, 38–43.
- Morales Vargas, R.E., Ya-umphan, P., Phumala-Morales, N., Komalamisra, N., Dujardin, J.-P., 2010. Climate associated size and shape changes in *Aedes aegypti* (Diptera: Culicidae) populations from Thailand. *Infect. Genet. Evol.* 10, 580–585.
- Morrison, A.C., Ferro, C., Pardo, R., Torres, M., Devlin, B., Wilson, M.L., Tesh, R.B., 1995. Seasonal Abundance of *Lutzomyia longipalpis* (Diptera: Phlebotomidae) at an endemic focus of visceral leishmaniasis in Colombia. *J. Med. Entomol.* 32, 538–548.
- Newton, E.A.C., Reiter, P., 1992. A model of the transmission of dengue fever with an evaluation of the impact of ultra-low volume (ULV) insecticide applications on dengue epidemics. *Am. J. Trop. Med. Hyg.* 47, 709–720.
- Nicholson, A.J., 1958. Dynamics of insect populations. *Annu. Rev. Entomol.* 3, 107–136.
- Nisbet, R.M., Gurney, W.S.C., 1976. Population dynamics in a periodically varying environment. *J. Theor. Biol.* 56, 459–475.
- Oki, M., Sunahara, T., Hashizume, M., Yamamoto, T., 2011. Optimal timing of insecticide fogging to minimize dengue cases: modeling dengue transmission among various seasonalities and transmission intensities. *PLoS Negl. Trop. Dis.* 5, e1367.
- Oo, T.T., Storch, V., Madon, M.B., Becker, N., 2011. Factors influencing the seasonal abundance of *Aedes (Stegomyia) aegypti* and the control strategy of dengue and dengue haemorrhagic fever in Thanlyin township, Yangon City, Myanmar. *Trop. Biomed.* 28, 302–311.
- Padmanabha, H., Soto, E., Mosquera, M., Lord, C.C., Lounibos, L.P., 2010. Ecological links between water storage behaviors and *Aedes aegypti* production: implications for dengue vector control in variable climates. *EcoHealth* 7, 78–90.
- Ponlawat, A., Harrington, L.C., 2007. Age and body size influence male sperm capacity of the dengue vector *Aedes aegypti* (Diptera: Culicidae). *J. Med. Entomol.* 44, 422–426.
- Predescu, M., Levins, R., Awerbuch-Friedlander, T., 2006. Analysis of a nonlinear system for community intervention in mosquito control. *Discret. Contin. Dyn. S.* 6, 605–622.
- Predescu, M., Sirbu, G., Levins, R., Awerbuch-Friedlander, T., 2007. On the dynamics of a deterministic and stochastic model for mosquito control. *Appl. Math. Lett.* 20, 919–925.
- Rahmstorf, S., Coumou, D., 2011. Increase of extreme events in a warming world. In: *Proceedings of the National Academy of Sciences*.
- Reisen, W.K., Milby, M.M., Bock, M.E., 1984. The effects of immature stress on selected events in the life history of *Culex tarsalis*. *Mosquito News* 44, 385–395.
- Reiter, P., 2007. Oviposition, dispersal, and survival in *Aedes aegypti*: implications for the efficacy of control strategies. *Vector Borne Zoonotic Dis.* 7, 261–273.
- Rios, A.A., Machado-Allison, C.E., Rabinovich, J.E., Rodriguez, D.J., 1978. Competencia intra e interespecifica en *Aedes aegypti* (L.) y *Culex fatigans* (Wiedemann) (Diptera: Culicidae) en condiciones de laboratorio. *Acta Cient. Venez.* 29, 467–472.
- Rodriguez, D.J., 1998. Time delays in density dependence are often not destabilizing. *J. Theor. Biol.* 191, 95–101.
- Ross, S.N., 1997. *Simulation. Statistical Modeling and Decision Science*. Harcourt-Academic Press, San Diego, CA, USA.
- Roy, M., Holt, R.D., Barfield, M., 2005. Temporal autocorrelation can enhance the persistence and abundance of metapopulations comprised of coupled sinks. *Am. Nat.* 166, 246–261.
- Rueda, L.M., Patel, K.J., Axtell, R.C., Stinner, R.E., 1990. Temperature-dependent development and survival rates of *Culex quinquefasciatus* and *Aedes aegypti* (Diptera: Culicidae). *J. Med. Entomol.* 27, 892–898.
- Salomon, O.D., Wilson, M.L., Munstermann, L.E., Travi, B.L., 2004. Spatial and temporal patterns of phlebotomine sand flies (Diptera: Phlebotomidae) in a cutaneous leishmaniasis focus in Northern Argentina. *J. Med. Entomol.* 41, 33–39.
- Schmalhausen, I.I., 1949. *Factors of Evolution; the Theory of Stabilizing Selection*. Blakiston Co., Philadelphia.
- Schneider, J.R., Morrison, A.C., Astete, H., Scott, T.W., Wilson, M.L., 2004. Adult size and distribution of *Aedes aegypti* (Diptera: Culicidae) associated with larval habitats in Iquitos, Peru. *J. Med. Entomol.* 41, 634–642.
- Schultz, G.W., 1993. Seasonal abundance of dengue vectors in Manila, Republic of the Philippines. *South East Asian J. Trop. Med. Public Health* 24, 369–375.
- Scott, T.W., Morrison, A.C., Lorenz, L.H., Clark, G.G., Strickman, D., Kittayapong, P., Zhou, H., Edman, J.D., 2000. Longitudinal studies of *Aedes aegypti* (Diptera: Culicidae) in Thailand and Puerto Rico: population dynamics. *J. Med. Entomol.* 37, 77–88.
- Shumway, R.H., Stoffer, D.S., 2000. *Time Series Analysis and its Applications*. Springer, New York.
- Sota, T., Mogi, M., Hayamizu, E., 1992. Seasonal distribution and habitat selection by *Aedes albopictus* and *Ae. triseriatus* (Diptera, Culicidae) in Northern Kyushu, Japan. *J. Med. Entomol.* 29, 296–304.
- Southwood, T.R.E., Tonn, R.J., Yasuno, M., Reader, P.M., Murdie, G., 1972. Studies on life budget of *Aedes aegypti* in Wat Samphaya, Bangkok, Thailand. *Bull. World Health Organ.* 46, 211–226.
- Stearns, S.C., 1981. On measuring fluctuating environments – predictability, constancy, and contingency. *Ecology* 62, 185–199.
- Stearns, S.C., 2000. Life history evolution: successes, limitations, and prospects. *Naturwissenschaften* 87, 476–486.
- Tonn, R.J., Macdonald, W.W., Sheppard, P.M., Jatanase, S., 1970. Magnitude of seasonal changes in larval populations of *Aedes aegypti* in Bangkok, Thailand. *Bull. World Health Organ.* 42, 943–950.

- Tsuda, Y., Takagi, M., 2001. Survival and development of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) larvae under a seasonally changing environment in Nagasaki, Japan. *Environ. Entomol.* 30, 855–860.
- Tuljapurkar, S., 1985. Population dynamics in variable environments. VI. Cyclical environments. *Theor. Popul. Biol.* 28, 1–17.
- Tuljapurkar, S., 1989. An uncertain life – demography in random-environments. *Theor. Popul. Biol.* 35, 227–294.
- Tuljapurkar, S.D., 1982. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theor. Popul. Biol.* 21, 114–140.
- Tun-Lin, W., Burkot, T.R., Kay, B.H., 2000. Effects of temperature and larval diet on development rates and survival of the dengue vector *Aedes aegypti* in north Queensland, Australia. *Med. Vet. Entomol.* 14, 31–37.
- Verdy, A., Caswell, H., 2008. Sensitivity analysis of reactive ecological dynamics. *Bull. Math. Biol.* 70, 1634–1659.
- Wada, Y., 1965. Effect of larval density on the development of *Aedes aegypti* (L.) and the size of adults. *Quaestiones Entomologicae* 1, 223–249.
- Wallner, W.E., 1987. Factors affecting insect population dynamics: differences between outbreak and non-outbreak species. *Annu. Rev. Entomol.* 32, 317–340.
- Walsh, R.K., Facchinelli, L., Ramsey, J.M., Bond, J.G., Gould, F., 2011. Assessing the impact of density dependence in field populations of *Aedes aegypti*. *J. Vector Ecol.* 36, 300–307.
- Wijeyaratne, P.M., Seawright, J.A., Weidhaas, D.E., 1974. Development and survival of a natural population of *Aedes aegypti*. *Mosquito News* 34, 36–42.
- Wilson, M.L., Agudelo-Silva, F., Spielman, A., 1990. Increased abundance, size, and longevity of food-deprived mosquito populations exposed to a fungal larvicide. *Am. J. Trop. Med. Hyg.* 43, 551–556.
- Wong, J., Morrison, A.C., Stoddard, S.T., Astete, H., Chu, Y.Y., Baseer, I., Scott, T.W., 2012. Linking oviposition site choice to offspring fitness in *Aedes aegypti*: consequences for targeted larval control of dengue vectors. *PLoS Negl. Trop. Dis.* 6, e1632.
- Yang, G.-J., Brook, B.W., Bradshaw, C.J.A., 2009a. Predicting the timing and magnitude of tropical mosquito population peaks for maximizing control efficiency. *PLoS Negl. Trop. Dis.* 3, e385.
- Yang, H.M., Macoris, M.L.G., Galvani, K.C., Andrighetti, M.T.M., Wanderley, D.M.V., 2009b. Assessing the effects of temperature on the population of *Aedes aegypti*, the vector of dengue. *Epidemiol. Infect.* 137, 1188–1202.