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

**Key-words:** population delay, density dependence, climate change, trade-offs, Lefkovitch matrix

## 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

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4 environmental changes and the occurrence of vector outbreaks. For example, in our  
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6 previous study we found a 10 week delay between extreme high temperature and the  
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8 occurrence of *Ae. aegypti* outbreaks, i.e., for the occurrence of abrupt increases in  
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10 mosquito abundance (Chaves et al. 2012). A plausible explanation for the occurrence of  
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12 delayed mosquito outbreaks following extreme weather events is the canalization of  
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14 environmental variability on population dynamics via changes in organism biology (e.g.,  
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16 development and physiology). These individual level changes can drive the dynamics of  
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18 population level demographic parameters as a strategy to cope with challenges arising  
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20 from a changing environment (Levins 1968; Schmalhausen 1949; Tuljapurkar 1989).  
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22 Here, we use a simple two-stage (larvae and adult) matrix model to ask if demographic  
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24 changes associated with particular environmental conditions could explain the delayed  
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26 association between temperature and *Ae. aegypti* population outbreaks. We simulate  
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28 the model using parameter estimated from a time series from Thailand (Chaves et al.  
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30 2012) and evaluate a series of sequential changes in demographic parameters for a  
31  
32 stochastic environment alternating between 'normal' and 'hot' conditions. Thus, unlike  
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34 our previous work, where an additive forcing function explained mosquito outbreaks  
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36 (Chaves et al. 2012), here we try to understand the emergence of mosquito outbreaks  
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38 as consequence of changes in *Ae. aegypti* demographic parameters that could be  
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40 triggered by the occurrence of unusual autocorrelated environments. We found that a  
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42 10-week lag maximum cross correlation, as observed in Thailand (Chaves et al. 2012),  
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44 is more likely to emerge in auto-correlated environments following sequential changes  
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46 in larval survival and adult fecundity, which decrease and increase, respectively, when  
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48 the environment is 'hot'. We conclude by discussing the importance of autocorrelated  
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4 environments for *Ae. aegypti* population outbreaks, the potential implications of changes  
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6 in individual mosquito traits, specially body size (Morales Vargas et al. 2010), on the  
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8 demographic changes we assumed to recreate the mosquito population outbreaks, and  
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10 the implications of our results for mosquito population management in changing  
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12 environments.  
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## 15 16 **2. Materials and Methods**

### 17 18 19 **2. 1. Data**

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23 Weekly mosquito density ( $N_t$ ) time series data (Fig. 1A) were obtained by  
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25 averaging *Ae. aegypti* abundance from 10 houses (out of a total of 23 monitored  
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27 houses) in Village 6 (13° 38' N, 101° 18' E) of Hua Samrong Tambon (subdistrict),  
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29 Plaeng Yao Amphoe (county), Chachoengsao (province) in Thailand using modified  
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31 vacuum cleaners from June 1990 to May 1993 (Scott et al. 2000). Samples were  
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33 restricted to houses because this is the main resting habitat of adult *Ae. aegypti*  
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35 (Christophers 1960; Scott et al. 2000). Maximum Temperature (TMAX) data (Fig. 1B)  
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37 were obtained from a weather station within a 20 KM radius of the site. We focus our  
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39 analysis on TMAX based in our previous results, which indicated a major role for this  
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41 climatic variable to explain *Ae aegypti* population dynamics in Thailand (Chaves et al.  
42  
43 2012). Seasonal patterns of rainfall and temperature range in Thailand were within the  
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45 range of recorded variability for the area (Chaves et al. 2012). See Scott et al. (2000)  
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47 for further details on study sites, sampling, and time series data.  
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### 54 55 **2.2. Time series descriptive statistical analysis**

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57 We examined the correlation structure of  $N_t$  and TMAX time series data using  
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59 standard techniques for time series analysis (Shumway & Stoffer 2000). These included  
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4 the autocorrelation function, **ACF**, the Partial ACF, **PACF**, (Fig. S1) and the cross-  
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6 correlation function, **CCF**, of TMAX pre-whitened residuals with residuals from a second  
7  
8 order autoregressive model; i.e., with two time lags based on the ACF and PACF of  $N_t$   
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10 (Fig. S1A and S1B). Further details about the times series analysis are presented in  
11  
12 Chaves et al (2012).  
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### 15 16 **2.3. Model and Simulations**

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19 In this section we briefly explain our model and simulation strategy to re-create  
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21 the emergence of a 10-week lag correlation between *Ae. aegypti*  $N_t$  and TMAX (Fig. 1D).  
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#### 23 24 **2.3.1. Model description**

25  
26 Let's assume that an adult mosquito population ( $N_t$ ) at time  $t$  is composed by  
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28 surviving adults ( $N_{t-1}$ ) and recruits from emerging larval individuals ( $J_{t-1}$ , which is a  
29  
30 mathematical abstraction of *Ae. aegypti* aquatic stages, i.e., eggs, larvae and pupae)  
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32 from the previous time step,  $t-1$ , as described by:  
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$$35 \quad N_t = sN_{t-1} + p J_{t-1} \quad (1)$$

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38 where  $s$  is the per-capita survival probability of adults and  $p$  is the per-capita survival  
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40 and emergence probability of larvae. Because *Aedes aegypti* larval developmental time  
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42 averages approximately a week for the temperatures observed in Thailand when the  
43  
44 data was collected (Bar-Zeev 1958b; Headlee 1940; Headlee 1941; Rueda et al. 1990;  
45  
46 Tun-Lin et al. 2000), we can further assume that larvae either emerge as adults, with  
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48 probability  $p$ , or die, with probability  $1-p$ , after one time step. Experiments and  
49  
50 entomological observations suggest that density-dependence regulation of *Aedes*  
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52 *aegypti* (Dye 1984; Gilpin & McClelland 1979; Legros et al. 2009; Southwood et al.  
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54 1972) occurs primarily during the immature stages. However, *Aedes aegypti* larval  
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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  $\theta$ , whose value is constrained in  $(0,1)$ , which in addition to a per capita fecundity rate ( $\lambda$ ), 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:

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

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



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4 stable, i.e., tends to recover to a fixed value following a disturbance (Levins & Wilson  
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6 1980). The model presented in (5) is reactive; i.e., prone to transiently amplify  
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8 disturbances (Caswell & Neubert 2005), in other words, a small increase in mosquito  
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10 abundance will grow transiently before the population returns to the equilibrium value  
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12 expected for the maximum likelihood parameter estimates obtained with the time series  
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14 described in the Data section (Table S1). For further details on model derivation,  
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16 sensitivity (i.e., response to changes in parameters), elasticity (i.e., response to  
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18 proportional changes in parameters), stability and reactivity analyses see Chaves et al  
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20 (2012).  
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### 25 26 27 **2.3.2. Simulation strategy**

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29 In the following paragraphs we explain the implementation and evaluation of  
30  
31 model simulations. We first define the considered stochastic environments, and then  
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33 discuss the selection of parameters used for the simulation, the sequential combination  
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35 of parameters employed to test different hypothesis about demographic parameter  
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37 change, and finally, the simulation protocol and the evaluation of the simulation results  
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39 that we performed.  
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#### 43 44 **2.3.2.1. Stochastic environments**

45  
46 Fig. 1D shows how mosquito abundance increased with high maximum  
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48 temperatures (TMAX), especially above 34°C (see also Table S1) suggesting that  
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50 mosquitoes have alternative strategies for dealing with “normal” ( $TMAX \leq 34^\circ C$ ) and  
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52 “hot” ( $TMAX > 34^\circ C$ ) environments. We inspected the maximum temperature time series  
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54 and determined that 25% of the time the environment was “hot”, while the remaining  
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56 75% of the time the environment was “normal”. Autocorrelation (Fig. S1C) and partial  
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4 autocorrelation (Fig. S1D) functions of TMAX, however, suggest that transitions  
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6 between the two environments are not-independent, because temperature data is  
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8 significantly autocorrelated, and indeed the transitions between normal and “hot”  
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10 environments occur with very heterogeneous probabilities (Table 1). Thus, for the  
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12 simulation of the stochastic environment we used the acceptance-rejection method  
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14 (Ross 1997) to generate environmental sequences of “normal” and “hot” environments  
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16 assuming that environments were correlated according to the probabilities presented in  
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18 Table 1. For comparison we also generated environmental sequences assuming the  
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20 two environments were independent, occurring with the probability of their frequency on  
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22 the TMAX time series data.  
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#### 28 29 *2.3.2.2. Parameters*

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31 In all simulations we employed parameter estimates from various sources. Adult  
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33 survival ( $s$ ) and the density-dependence exponent ( $\theta$ ) were estimated from the time  
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35 series and kept constant in all simulations (Table S1). We also kept these parameters  
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37 constant for biological reasons. Adult mosquitoes have an increased autonomy from the  
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39 environment by their flying ability, which allows them to disperse in adverse  
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41 environments (Edman et al. 1998), probably keeping adult survival ( $s$ ) constant  
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43 (Christophers 1960). Population dynamics are very sensitive to small changes in  $\theta$   
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45 (Chaves et al. 2012), which in principle makes us believe this parameter has low  
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47 variability, a fact further reinforced by the similarity in estimates from populations as far  
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49 apart as Puerto Rico and Thailand (Chaves et al. 2012). Based on entomological  
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51 observations (Bar-Zeev 1958a; Tun-Lin et al. 2000; Walsh et al. 2011; Wijeyaratne et al.  
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53 1974; Yang et al. 2009b) we assumed that high temperatures were detrimental for  
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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; Headlee 1941; Koenraad 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 ( $\widehat{\lambda p}$ , 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 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 ( $\lambda_1 p_1 = \lambda_2 p_2 = \widehat{\lambda p}$ ). 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:

$$N^* + Exo = s(N^*) + p_2 \lambda_3 (N^*)^\theta \quad (6)$$

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4 for  $\lambda_3$ . Taking the average estimated forcing for the “hot” environments ( $\widehat{Exo} = 3.6$ ) we  
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7 estimated the following overcompensated fecundity ( $\lambda_3 = 8.48$ ). In a set of simulations  
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10 we also assumed the presence of further environmental noise, which is defined as  
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12 perturbations affecting all individuals in a population at a given time (Mangel 2006).  
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14 Under this assumption, the right hand side of equations (4) is log-transformed (Dennis &  
15  
16 Taper 1994), and the resulting left hand side of the equation,  $z_t$ , is assumed to be  
17  
18 normal, i.e.,  $z_t \sim N(\log(N_t), \sigma_{envs}^2)$ , where  $\sigma_{envs}^2 = 0.181$  was estimated from the time  
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20 series (Table S1). Table 2 shows the parameters we employed in the simulations.  
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### 24 **2.3.2.3. Sequential demographic parameter changes for transitions between normal and** 25 26 **“hot” environments**

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29 The transition probability from “normal” to “hot” environments renders the  
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31 estimation of an average timespan for “hot” environments, which can be assumed to  
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33 have a geometric distribution. The environmental change from “hot” back to normal can  
34  
35 be seen as the time to the first failure in a series of Bernoulli trials (Mangel 2006). From  
36  
37 Table 1, it can be estimated that on average a hot environment should last around 6  
38  
39 weeks (i.e.,  $1/\text{probability of changing to normal given the environment is “hot”}$ ). With this  
40  
41 information we defined 8 sequences of larval survival ( $p$ ) and fecundity ( $\lambda$ ) changes  
42  
43 shorter than 6 weeks (Table 3) to test each sequence ability to generate a 10 week  
44  
45 delayed association between TMAX and mosquito population size. Briefly, case 1 and 2  
46  
47 are controls where the transition from a “normal” to “hot” environment decreases  $p$  and  
48  
49 increases  $\lambda$  to compensate (case 1) or over-compensate (case 2) the change in  $p$ . In  
50  
51 case 3 following the transition to a “hot” environment  $p$  decreased and after one week  $\lambda$   
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53 increased in a compensatory manner. Case 4 is similar to 3 but after the transition to a  
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4 normal environment the increased fecundity of the hot environment last 1 week. Case 5  
5 is similar to case 4, but after the compensation in the “hot” environment  $\lambda$  further  
6  
7 increases to over-compensatory. In case 6  $p$  decreases following the transition to a “hot”  
8  
9 environment, but then increases (to a value below the one for the “normal” environment)  
10  
11 together with  $\lambda$  which also becomes over-compensatory. Finally, cases 7 and 8 consider  
12  
13 a two-step change in  $p$  (larval survival decreases and then recovers, yet is smaller than  
14  
15 before the advent of the hot environment) and also in  $\lambda$  (fecundity compensates for the  
16  
17 change in survival before increasing to an over-compensatory level). In case 8 over-  
18  
19 compensatory  $\lambda$  spans two weeks once the environment is back to “normal”.  
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#### 25 26 **2.3.2.4. Simulation protocol**

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28 For each one of the cases in Table 3 we generated 1000 replications of random  
29  
30 environments that were 1200 week long. Each replicate was used to iterate equation (4),  
31  
32 where the initial conditions were the estimated larval and adult population at the non-  
33  
34 trivial equilibrium of equation (4); i.e., when  $N^* \neq 0$ , for the parameters presented in  
35  
36 Table S1, and parameters for a given environment changed according to the rules  
37  
38 defined in Table 3. We keep the last 180 values of population size and the environment  
39  
40 and computed the cross correlation function between these two variables for 19 lags  
41  
42 (lag -19 to +19). We also computed the mean, maximum, 25<sup>th</sup> and 75<sup>th</sup> quantiles,  
43  
44 variance, skewness and kurtosis of the simulated mosquito abundance time series, as  
45  
46 well as the average environment using scores presented in Table 3. We also performed  
47  
48 this protocol assuming the presence of environmental noise and for Case 2 assuming  
49  
50 an independent environment (see section 2.3.2.1)  
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#### 57 58 **2.3.2.5. Evaluation of the simulation results**

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

### 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 **3. Results**

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50 Fig. 2 shows the results from simulations assuming independent and  
51 autocorrelated environments. Fig. 2A shows that independent environments invariably  
52 lead to a 2 week lag maximum cross correlation between TMAX and  $N_t$ . For the  
53 autocorrelated environment (Fig. 2B) the lag for the maximum CCF between TMAX and  
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4  $N_t$  occurs between 1 and 3 weeks. The addition of environmental noise leads to a 1  
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6 week lag maximum cross correlation between TMAX and  $N_t$  in an independent  
7  
8 environment (Fig. 2C). Environmental noise also generates a distribution where the  
9  
10 probability of 0 week lag becomes maximum in the autocorrelated environment (Fig.  
11  
12 2D). Environmental noise in an autocorrelated environment also generates a probability  
13  
14 distribution where association between mosquito abundance and TMAX for lags of 4  
15  
16 weeks or more (Fig. 2D) is more likely to occur than when noise is present in  
17  
18 independent environments (Fig. 2C). Here, it is important to highlight that in Fig. 2  
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20 probability for negative  $\rho$ , lag correlation and 12+ are cumulative for several lags. Thus,  
21  
22 this preliminary comparison between independent and autocorrelated environments  
23  
24 suggests that autocorrelated environments can delay the lag of the association between  
25  
26 TMAX and  $N_t$ .  
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33 Fig. 3 shows the result for the sequence of changes in demographic parameters  
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35 that maximized the probability of a 10 week lag maximum CCF, which was case 6 of  
36  
37 Table 3. In general the probability of 10 week lag having the maximum CCF was very  
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39 low, slightly above 2 % in the best cases, being maximal for  $p_3 = 0.10$  (Fig. 3A). For the  
40  
41 case of  $p_3 = 0.10$  the maximum CCF occurred at 5 weeks of lag (Fig. 3B). It is worth  
42  
43 noticing that maximum CCF at 5 weeks of lag was independent of  $p_3$  (Fig. 3C). However,  
44  
45 the correlation at 10 week of lag emerged only when environmental noise was  
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47 considered, being maximized when  $p_2 > p_3$ , and maximized for higher lags when  
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49  $p_3 = 0.10$  (Fig. 3D). Interestingly case 6 of Table 3 had the highest probability to  
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51 produce the longest delays for the maximum CCF, both assuming stochastic  
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4 environments (for comparison with other cases see Fig. S2) and stochastic  
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6 environments with environmental noise (for comparison with other cases see Fig. S3).  
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9 Fig. 4 shows a detailed evaluation of simulation results from case 6 (Table 3)  
10 assuming a stochastic and autocorrelated environment with environmental noise. Fig.  
11 4A presents the distribution of the observations from Thailand, which shows the  
12 abundance to be positively skewed with frequent mosquito outbreaks. Fig. 4B to 4H  
13 show the distribution of the simulation outputs for the mean (Fig. 4B), maxima (Fig. 4C),  
14 25<sup>th</sup> (Fig. 4D) and 75<sup>th</sup> (Fig. 4E) quantiles, variance (Fig. 4F), skewness (Fig. 4G) and  
15 kurtosis (Fig. 4H). In all cases the observed values from the original time series were  
16 inside the 95 % non-extreme outputs of the simulations (i.e, within the 2.5 and 97.5  
17 quantiles of the empirical distributions from simulation estimates), indicating the success  
18 of the model not only to generate the 10 week delayed maximum CCF between TMAX  
19 and  $N_t$ , but also the different moments and 25<sup>th</sup> and 75<sup>th</sup> quantiles of the observed  
20 distribution at Village 6, Chachoengsao, Thailand. Fig. 4I shows the size of the 75<sup>th</sup>  
21 quantile of the simulations distribution as function of the average environment, showing  
22 a linear increase of this quantile [a proxy measurement of mosquito outbreaks] with the  
23 average environment.  
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45 In summary, our results showed that autocorrelated stochastic environments,  
46 environmental noise and sequential changes in demographic parameters could  
47 generate a 10 week delay in the association between increased temperatures and  
48 mosquito outbreaks, a pattern observed in Thailand (Fig. 1). Delays emerged following  
49 sequential changes in demographic parameters after the onset of “hot” environments,  
50 specifically: 1) a decreased larvae survival; 2) an over-compensatory fecundity increase  
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4 that lasts until the environment returns to “normal”; 3) a larvae survival increase when  
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6 the environment returns to “normal”, 3) a fecundity decrease to its original value  
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8 following the increase in larval survival once in the “normal” environment.  
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## 10 11 **4. Discussion**

### 12 13 **4.1. Hot environments and mosquito outbreaks**

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15 Sudden extraordinary changes in species abundance (i.e., outbreaks), have  
16  
17 been mostly studied in insects, primarily agricultural pests (Berryman & Stark 1985), but  
18  
19 also medically important species, especially mosquitoes (Chase & Knight 2003; Yang et  
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21 al. 2009a). In fact, it could be argued that insect outbreaks have underpinned the wider  
22  
23 ecological discussion on whether populations undergo density dependent-regulation  
24  
25 (Chaves & Koenraadt 2010; Nicholson 1958). In the applied context of disease control,  
26  
27 vector outbreaks are of major importance given density-dependence implications for  
28  
29 different control measures, such as larviciding (Agudelo-Silva & Spielman 1984; Wilson  
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31 et al. 1990), insecticide spraying (Newton & Reiter 1992; Oki et al. 2011), and more  
32  
33 recently, the field release of genetically modified mosquitoes (Legros et al. 2009; Magori  
34  
35 et al. 2009).

36  
37 Here, we tried to understand the association between extreme weather and  
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39 mosquito outbreaks in a population with clear signatures of density-dependence  
40  
41 (Chaves et al. 2012; Dye 1984; Southwood et al. 1972). Our previous analysis showed  
42  
43 that extreme “hot” temperatures (above 34 °C) were associated with delayed outbreaks  
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45 of *Ae. aegypti*, in a very localized fashion, yet our study did not fully explain the  
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47 emergence of a 10 week delay in the association between extreme “hot” temperatures  
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49 and unusually large mosquito abundance (Chaves et al. 2012). In our previous study we  
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4 accounted for this localized association between extreme temperatures and mosquito  
5 outbreaks by adding a non-linear function of temperature to a density-dependent  
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7 delayed recruitment model. Nevertheless, as clearly noted by Schmalhausen (1949)  
8  
9 and Levins (1968) the impacts of the changing environments are canalized by the  
10 individuals, i.e., demographic parameters are likely to change in order to ensure  
11 population persistence in a different environment (Tuljapurkar 1985; Tuljapurkar 1989).  
12  
13 In the case of rainfall, association delays tend to be shorter, between 1 and 4 weeks  
14 (Barrera et al. 2011; Scott et al. 2000) and it can be argued that changes in adult  
15 recruitment by rainfall induced generation of larval habitats could underlie the outbreaks  
16 (Chase & Knight 2003; Chaves et al. 2012; Yang et al. 2009a). In this sense, rainfall  
17 and associated changes in relative humidity could ease mosquito dispersal (Edman et  
18 al. 1998) which maybe essential for population persistence even if local mosquito larval  
19 sources are not viable, as suggested by metapopulation persistence of locally inviable  
20 populations in models that consider dispersal in autocorrelated environments (Roy et al.  
21 2005). By contrast, hot temperatures are known to increase larval mortality in *Ae.*  
22 *aegypti* (Bar-Zeev 1958a; Mohammed & Chadee 2011), as well as other mosquitoes  
23 (Chaves et al. 2011). These observations imply that a series of compensatory or over-  
24 compensatory changes in life history traits (e.g., fecundity compensating changes in  
25 survival) could be expected if mosquito life history is governed by fitness trade-offs  
26 (Stearns 2000). In that sense our model simulations suggest that an increase in  
27 temperature could be linked with both a decrease in larval survival and an over-  
28 compensatory increase in fecundity, a result indirectly suggested by the potential fitness  
29 increase of emerging *Ae aegypti* adults from larvae subjected to external mortality  
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4 (Wilson et al. 1990). We also found the correlated structure of the environment to be  
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6 important for the generation of delayed mosquito outbreaks. A model under the  
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8 assumption of independent environmental transitions was unable to re-create the delay  
9  
10 between extreme hot temperatures and mosquito outbreaks. Moreover, the assumption  
11  
12 of environmental independence is likely wrong because both the ACF of TMAX  
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14 indicates that TMAX has an auto-correlated nature (Fig. S1C and S1D).  
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19 Our model simulations also suggest the emergence of delayed outbreaks to be  
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21 linked with sequential changes in demographic parameters following the onset of “hot”  
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23 environments. This result has implications for entomological and modeling research.  
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25 Previous studies have shown that mosquitoes do change their phenotypes following  
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27 environmental fluctuations. For example, changes have been observed in body size,  
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29 which tends to be larger at low temperatures (Scott et al. 2000; Tsuda & Takagi 2001).  
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31 Mosquito body size is positively associated with fecundity (Bar-Zeev 1957), male sperm  
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33 quality (Ponlawat & Harrington 2007), survival (Tsuda & Takagi 2001) and overall  
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35 fitness (Koenraadt 2008), a pattern shared by other mosquito species (Reisen et al.  
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37 1984). How these changes correlate with a given population demographic parameters  
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39 or if they are progressive after the onset of relatively stable environmental conditions is  
40  
41 an open question (Stearns 1981). We also want to emphasize that our results likely  
42  
43 derive from specific sequential changes in life history traits, because for the same fixed  
44  
45 parameters the delayed pattern only emerged with a given sequence of changes, in  
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47 parameters whose proportional changes have relative little impact on the dynamics as  
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49 revealed by a perturbation (i.e., parameter sensitivity and elasticity) analysis we  
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51 performed in our previous study of this model (Chaves et al. 2012). In that sense,  
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4 parameter estimates from different environmental conditions, based on semi-natural  
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6 experiments in heterogeneous and fluctuating environments (Carrington et al. 2013;  
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8 Chaves et al. 2011), would help to better understand the impacts of temperature on  
9  
10 larval survival and the associated changes or trade-offs with fecundity (Stearns 2000).  
11  
12 Ultimately, this entomological research could provide a basis to test the existence of  
13  
14 sequential changes in life history traits with the advent of “hot” environments, a  
15  
16 phenomenon that is becoming increasingly more frequent worldwide (Hansen et al.  
17  
18 2012; Rahmstorf & Coumou 2011). From the modeling perspective, analytical results for  
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20 population growth in autocorrelated environments (Tuljapurkar 1982) need to be  
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22 extended to non-linear (density-dependent) cases or generalized for non-Markovian  
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24 situations (where memory goes beyond the previous time step in discrete time models).  
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31 A detailed dissection of delays in the association between extreme high  
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33 temperatures and mosquito outbreaks in light of ecological theory suggest that they  
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35 could emerge by the joint action of several factors. First, as originally noticed by Dye  
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37 (1984) the delayed recruitment of adults can lead to generational cycles (May et al.  
38  
39 1974). Although our model also considers delayed adult recruitment (Chaves et al.  
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41 2012), this feature alone cannot explain mosquito outbreaks, nor the localized nature of  
42  
43 the association between high temperatures and the outbreaks. Moreover, generational  
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45 delays often do not destabilize equilibria in stage-structured models (Rodriguez 1998),  
46  
47 and our model is numerically stable for the parameters we employed in the simulations,  
48  
49 and structurally stable when density-dependence exists, i.e.,  $\theta < 1$  (Chaves et al. 2012).  
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51 Nevertheless, our model is reactive, thus able to transiently amplify perturbations and  
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53 generate the autocorrelation patterns we observed in the mosquito abundance time  
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4 series data (Chaves et al. 2012). The introduction of sequential and over-compensatory  
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6 changes in the life history of *Ae aegypti* could lengthen the delay of the association  
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8 beyond what can be attributed to a reactive response, with an average of 4 to 5 weeks  
9  
10 (Figure 3C & 3D). These environmentally forced “cycles” can then be amplified if they  
11  
12 coincide with reactive response in the model, a result independently derived for matrix  
13  
14 models (Costantino et al. 1998; Tuljapurkar 1985) and ordinary differential equations  
15  
16 (Nisbet & Gurney 1976). In fact, the 5 week cycles can resonate and generate  
17  
18 association delays of sub-harmonic length (i.e., a multiple of 4 or 5 weeks), for example  
19  
20 10 weeks. In our simulations, however, resonance alone by the stochastic environment  
21  
22 could only lengthen the association delay to 8 weeks, with the emergence of 10 week  
23  
24 delay association only observed when additional environmental noise was considered.  
25  
26 In fact, the additional environmental noise can be amplified by the reactive nature of the  
27  
28 model (Verdy & Caswell 2008). The nature of the additional environmental noise could  
29  
30 be related to other environmental factors. For example, mosquito wing size was  
31  
32 primarily correlated with relative humidity (Morales Vargas et al. 2010), indicating that  
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34 beyond temperature, mosquito development and body size could be sensitive to many  
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36 factors.  
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#### 45 **4. 2. Implications for control**

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47 Our results suggest that more variable temperature regimes and extended “hot”  
48  
49 environments could be associated with increased mosquito outbreaks. This feature is  
50  
51 common to other insects, where variable environments can lead to larger average  
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53 population size when compared with stable environments (Costantino et al. 1998). In  
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55 that sense, forecasts concerning unusual temperature increases could help to  
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4 temporally target interventions of highly productive larval developmental containers  
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6 (Maciel-de-Freitas & Lourenco-de-Oliveira 2011) and other refugia that potentially  
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8 promote mosquito outbreaks (Wallner 1987). The advent of “hot” environments is a time  
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10 when interventions can be highly successful in diminishing the entomological risk of  
11  
12 disease transmission by *Ae aegypti*. Nevertheless, a challenge is that such times can  
13  
14 be associated with decreased interest on implementing an intervention given the high  
15  
16 likelihood of decreased mosquito abundance and nuisance (Predescu et al. 2006).  
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### 21 **4. 3. Synthesis**

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23 Model simulations showed that mosquito outbreaks are likely the product of  
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25 reactive population dynamics and over-compensatory fecundity following increased  
26  
27 larval mortality in auto-correlated environments. In more variable environments, where  
28  
29 transitions to the “hot” environment are more prevalent, we can expect an increased  
30  
31 occurrence of *Ae aegypti* outbreaks. Control strategies could benefit from targeting  
32  
33 highly productive mosquito refugia during “hot” periods even if mosquito abundance is  
34  
35 nil, especially because a temperature shift might signal upcoming outbreak. Control  
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37 interventions at these times, even if counterintuitive given the likely low mosquito  
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39 density, could decrease *Ae. aegypti* population expansion and its associated  
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41 entomological risk for increased pathogen transmission.  
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## Figure Legends

**Figure 1 Data (A)** Weekly adult *Aedes aegypti* abundance,  $N_t$ , from Village 6, Chachoengsao, Thailand (June 1990 - May 1993) **(B)** Weekly maximum temperature, TMAX (°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<sub>t-10</sub> (°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 grey line indicates the 10 week delayed “Hot” environment (10 WD Hot).

**Figure 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 ( $\lambda$ ) 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.

**Figure 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+” grey 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 grey tone indicates a lower correlation. For reference, the best life history parameter transition sequence is case 6 in Table 3.

**Figure 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 25<sup>th</sup> and 75<sup>th</sup> quantiles (qt) of the distribution. **(B)** Smoothed probability density (SPD) of the mean  $N_t$ . In this and subsequent panels grey 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  $N_t$  25<sup>th</sup> quantile **(E)** SPD of  $N_t$  75<sup>th</sup> quantile **(F)** SPD of  $N_t$  variance **(G)** SPD of  $N_t$  skewness **(H)** SPD of  $N_t$  kurtosis **(I)**  $N_t$  75<sup>th</sup> quantile as function of the average environment

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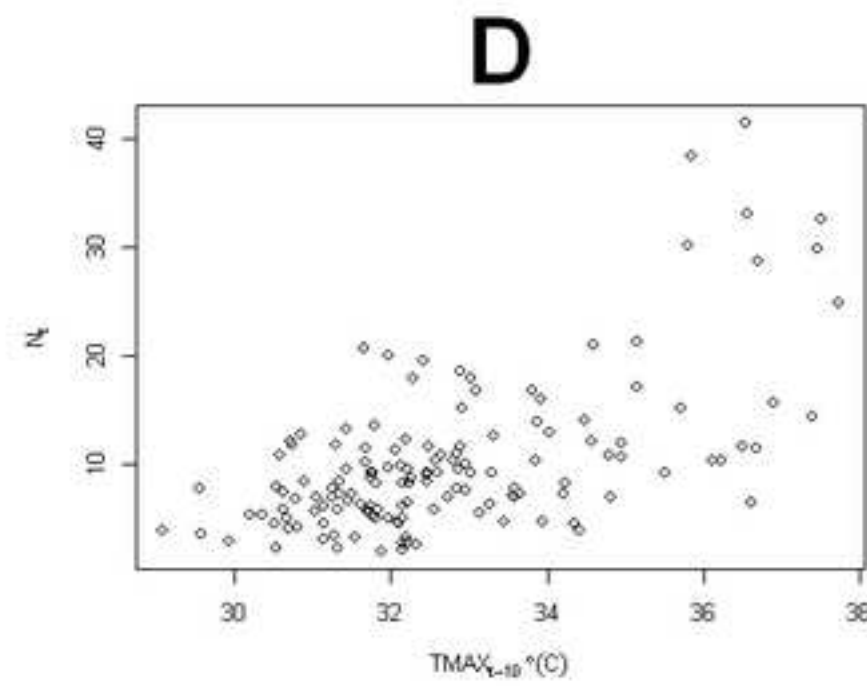
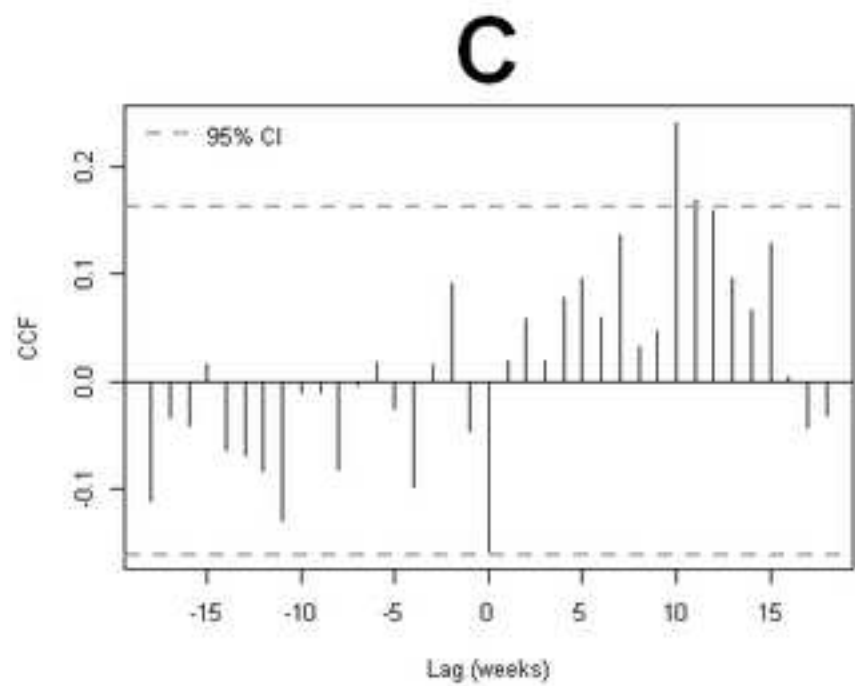
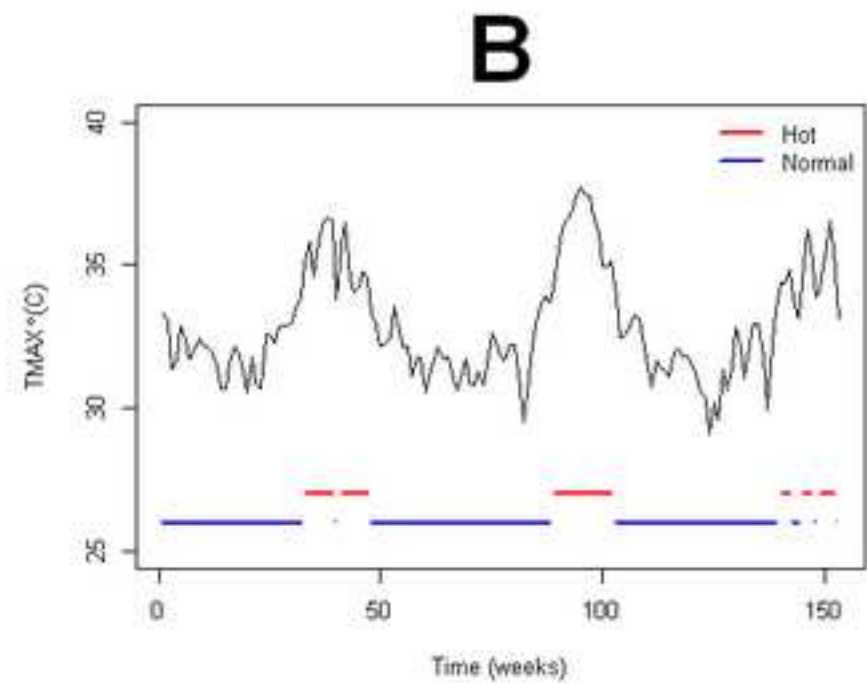
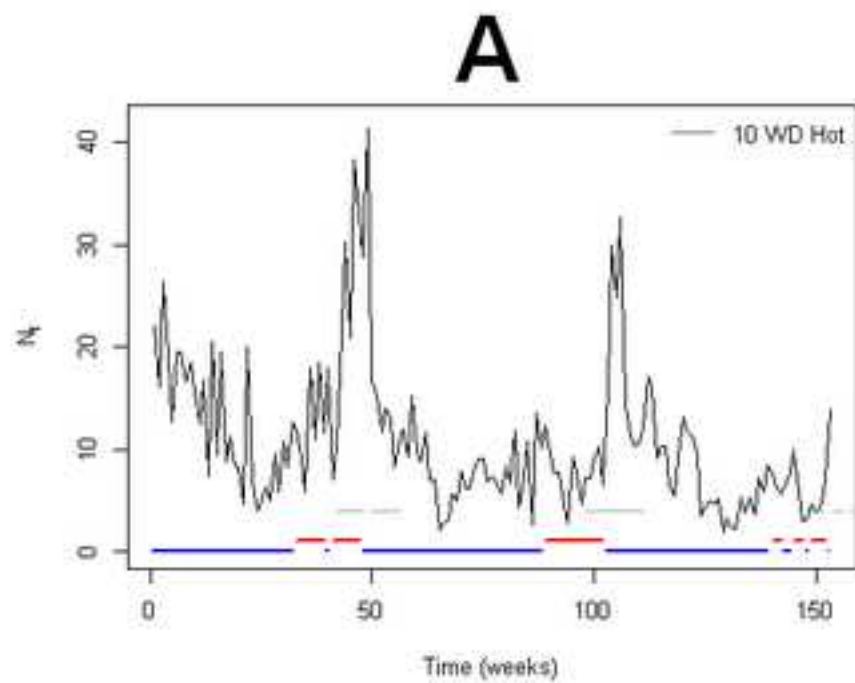


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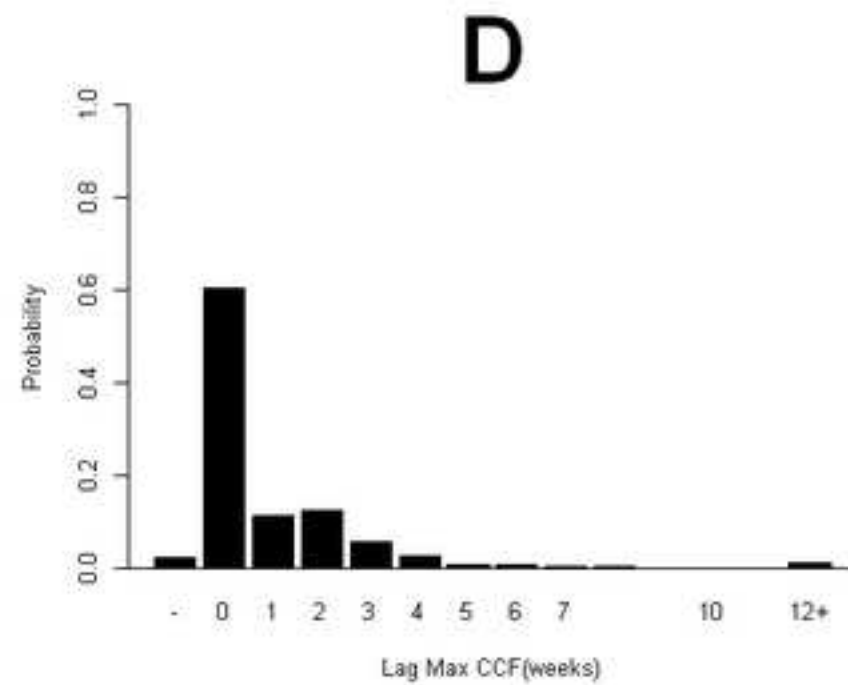
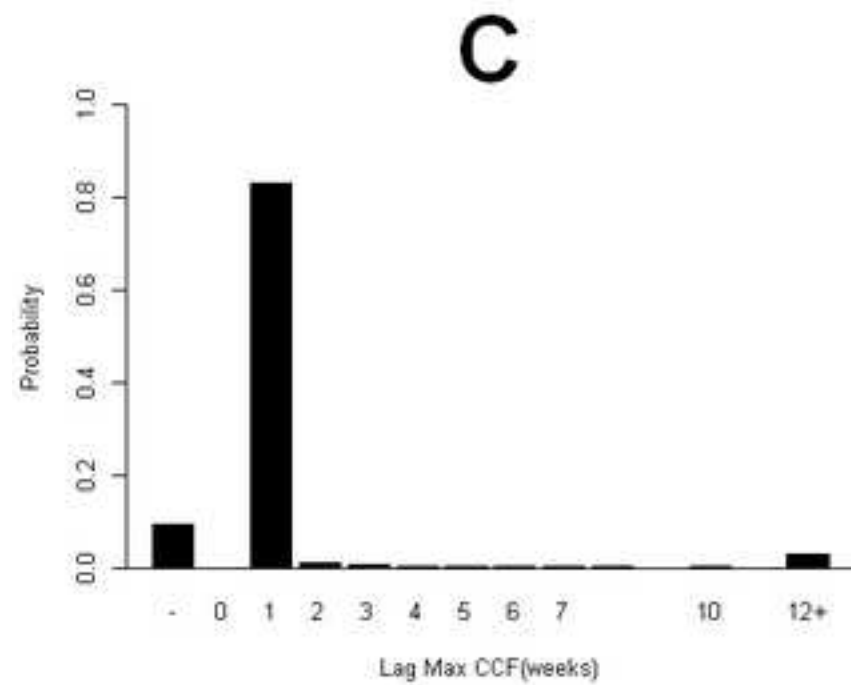
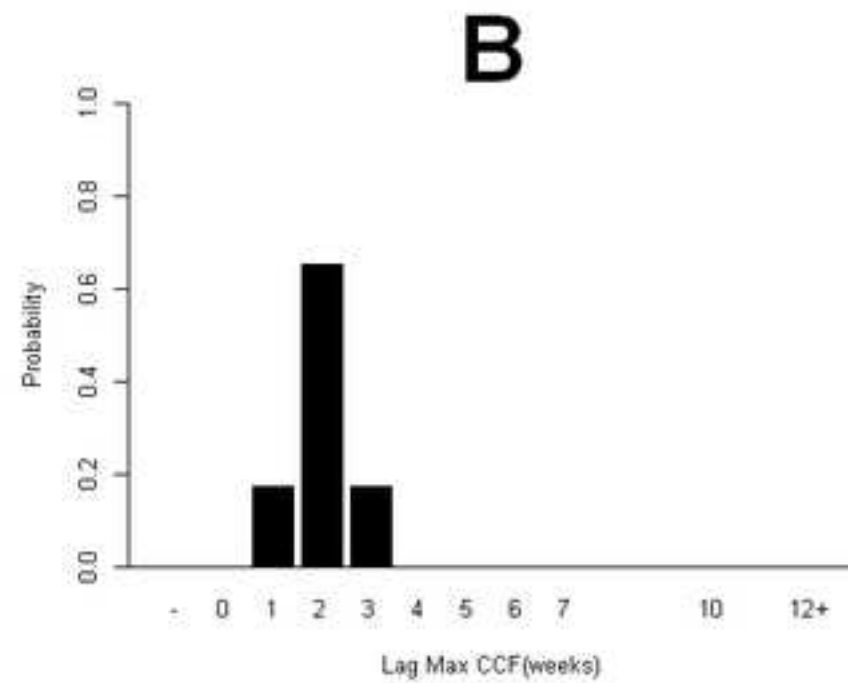
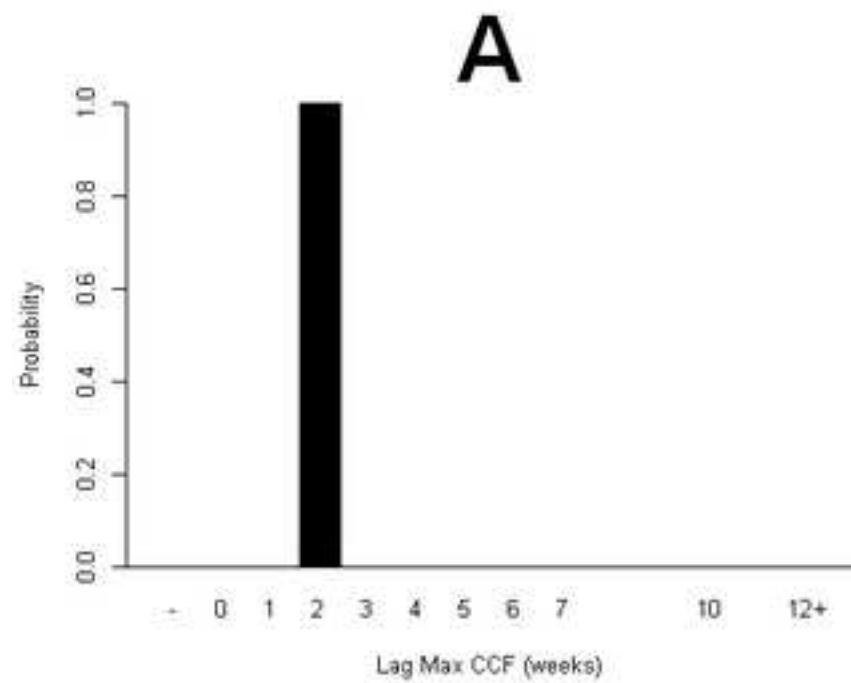


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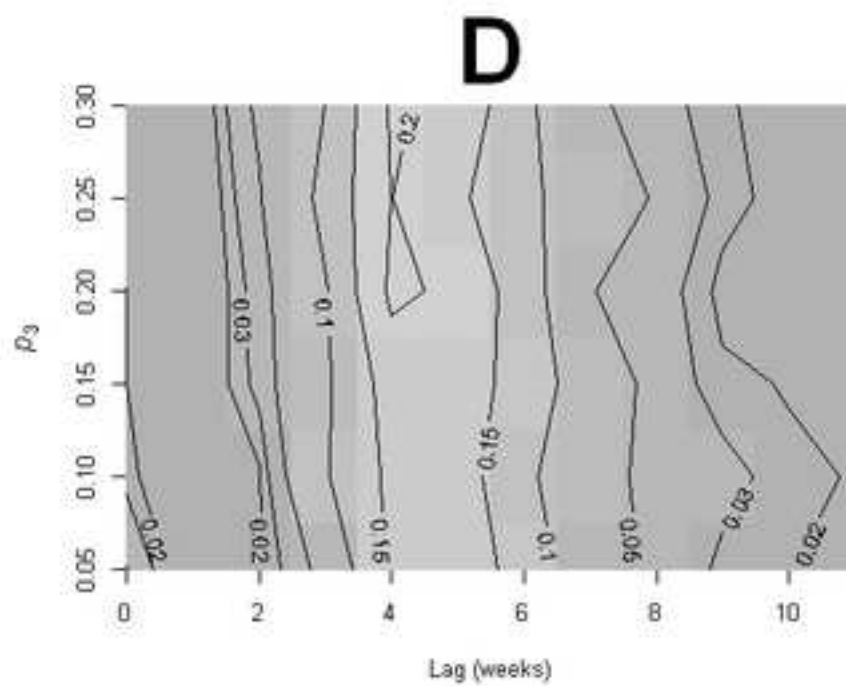
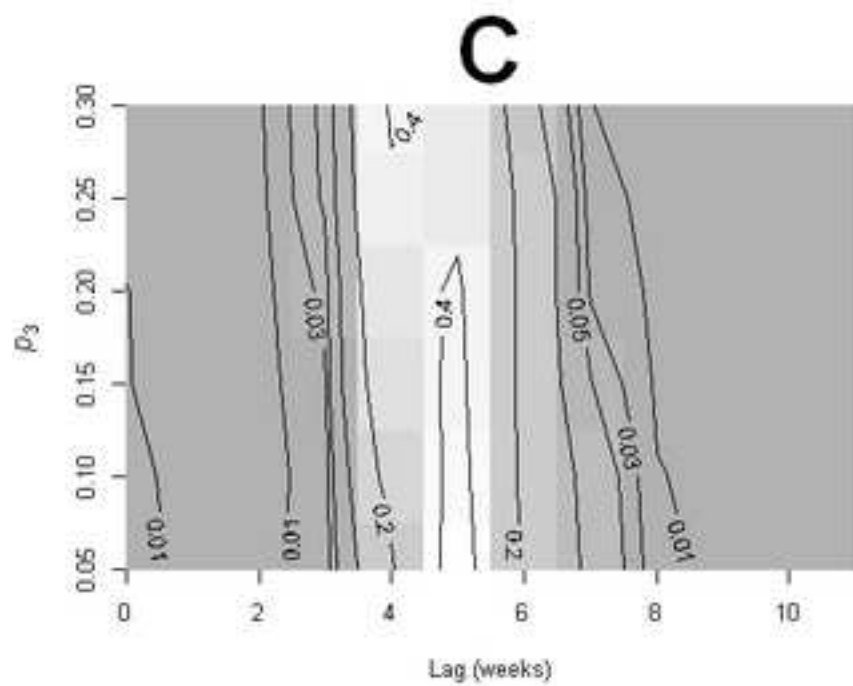
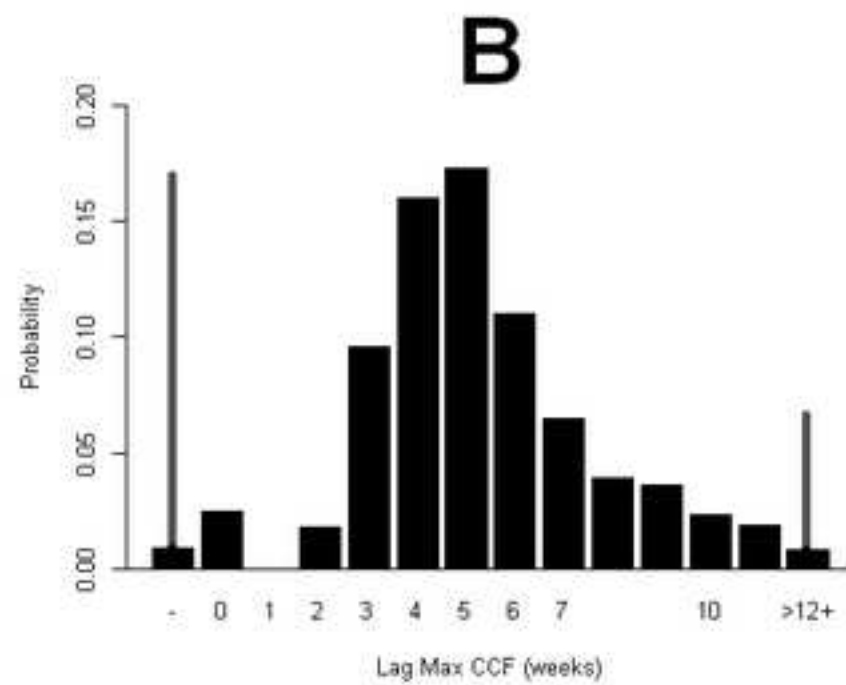
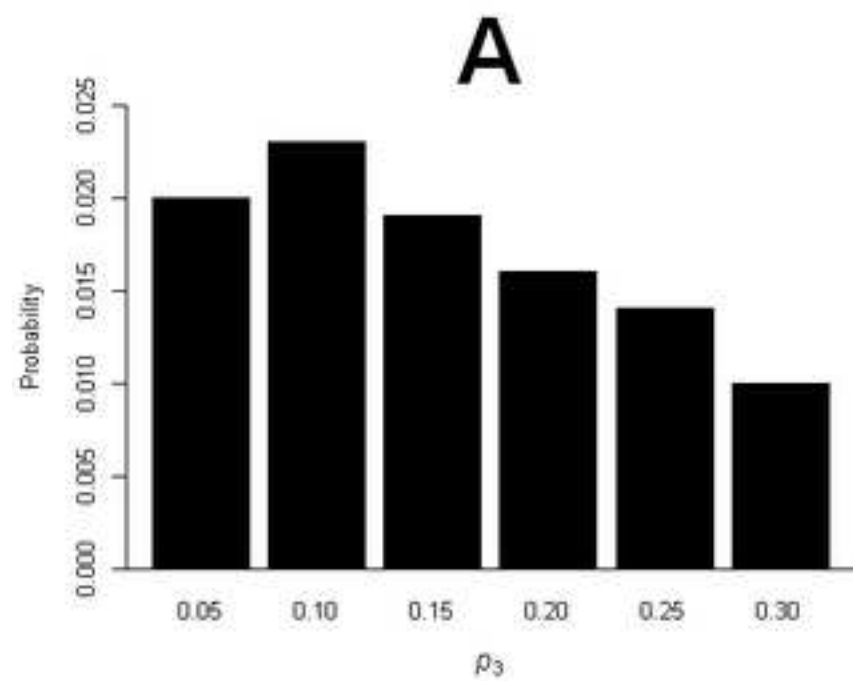
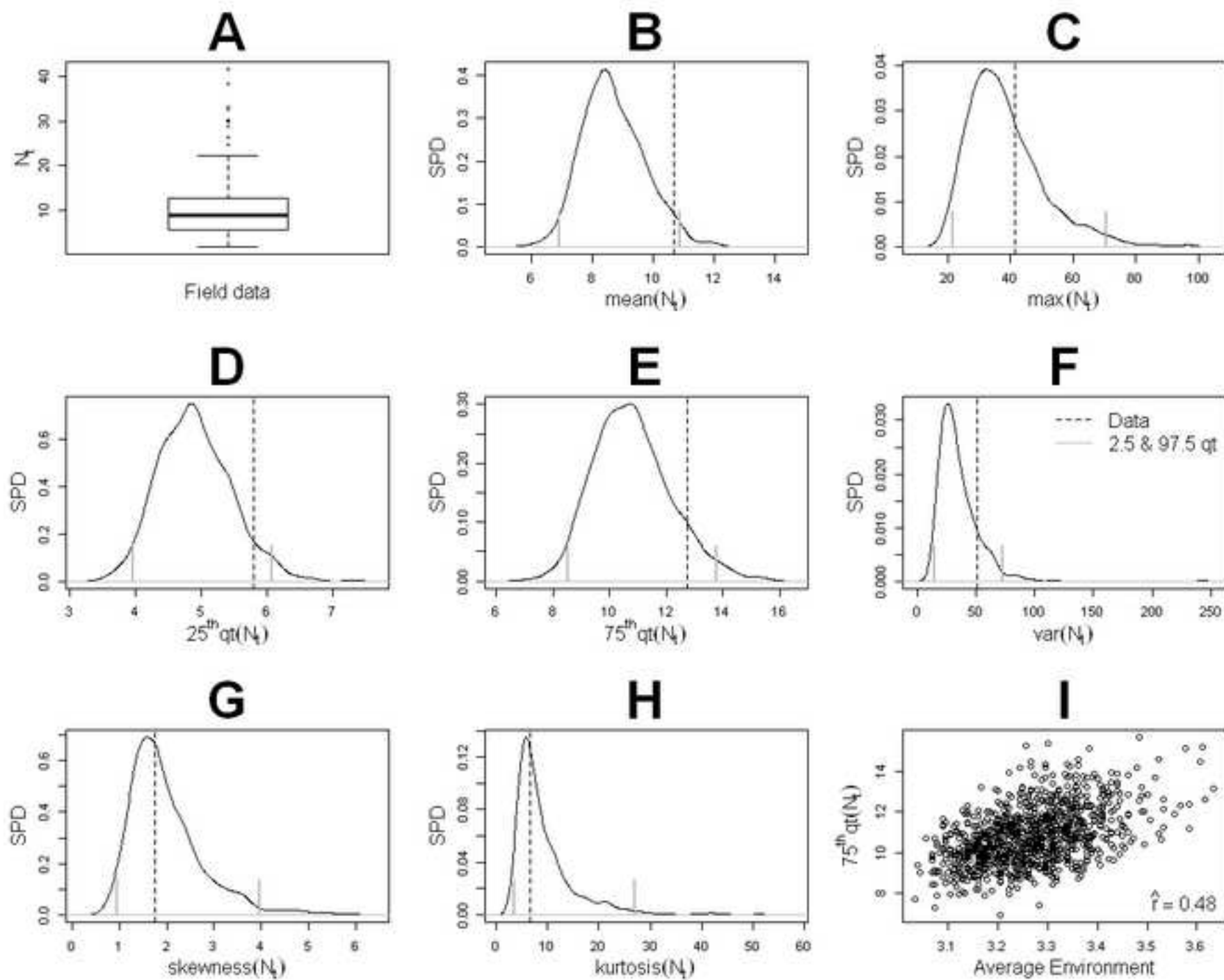




Figure 4  
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**Table 1** Frequency and probability of transition between “hot” (average weekly maximum temperature > 34.03° C) and normal environments in Village 6, Chachoengsao, Thailand. Conditional probability indicates the probability of changing 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

**Table 2 Parameters employed in the simulations**

<b>Parameter</b>	<b>Estimate</b>	<b>Source</b>
Adult Survival (s)	0.317	(Chaves et al. 2012)
Denso-dependence exponent ( $\theta$ )	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 ( $\lambda$ )	$\lambda_1 = 3.42$ $\lambda_2 = 6.84$ $\lambda_3 = 8.48$	(Chaves et al. 2012) <sup>a</sup>
Variance of the environmental noise ( $\sigma_{envs}^2$ )	0.181	(Chaves et al. 2012)

<sup>a</sup>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.

**Table 3** Larval survival ( $p_i$ ) and fecundity ( $\lambda_i$ ) 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  $\lambda_i$  for  $i \in \{1,2,3\}$ . In cases 5 to 8 the exogenous forcing is included through an over-compensatory fecundity ( $\lambda_3$ ).

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	$\lambda_1, p_1(3)$	$\lambda_1, p_3(1)$	$\lambda_2, p_3(2)$	$\lambda_2, p_2(4)$	$\lambda_3, p_2(5)$	...	$\lambda_3, p_2(5)$	$\lambda_3, p_1(6)$	$\lambda_1, p_1(3)$
Case 8	$\lambda_1, p_1(3)$	$\lambda_1, p_3(1)$	$\lambda_2, p_3(2)$	$\lambda_2, p_2(4)$	$\lambda_3, p_2(5)$	...	$\lambda_3, p_2(5)$	$\lambda_3, p_1(6)$	$\lambda_3, p_1(6)$