A stochastic population dynamics model for *Aedes aegypti*: formulation and application to a city with temperate climate

Marcelo Otero, Hernán G Solari *

Department of Physics, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires

Nicolás Schweigmann

Department of Genetics and Ecology, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires

Abstract

Aedes aegypti is the main vector for dengue and urban yellow fever. It is extended around the world not only in the tropical regions but also beyond them, reaching temperate climates. Because of its importance as a vector of deadly diseases, the significance of its distribution in urban areas and the possibility of breeding in laboratory facilities, *Aedes aegypti* is one of the best-known mosquitoes. In this work the biology of *Aedes aegypti* is incorporated into the framework of a stochastic population dynamics model able to handle seasonal and total extinction as well as endemic situations. The model incorporates explicitly the dependence with temperature. The ecological parameters of the model are tuned to the present populations of *Aedes aegypti* in Buenos Aires city, which is at the border of the present day geographical distribution in South America. Temperature thresholds for the mosquito survival are computed as a function of average yearly temperature and seasonal variation as well as breeding site availability. The stochastic analysis suggests that the southern limit of *Aedes aegypti* distribution in South America is close to the 15°C average yearly isotherm, which accounts for the historical and current distribution better than the traditional criterion of the winter (July) 10°C isotherm.

Key words: mathematical ecology, population dynamics, *Aedes aegypti*, stochastic model, temperate climate

* Corresponding author:Hernán G Solari
  Email address: `solari@df.uba.ar` (Hernán G Solari).

1 Introduction

Aedes aegypti is mostly a domestic mosquito and the primary vector for urban yellow fever and dengue. It is the most important vector for dengue in the Americas, and it can be found in tropical and subtropical regions such as Florida, Central America, the Caribbean Islands and Brazil. It is estimated that about 2500-3000 millions of people live in areas where the transmission of the dengue virus is endemic.

The limits for the geographical distribution of *Aedes aegypti* tentatively adopted by Christophers (1960), and reproduced by several authors [WHO (1998); FUNCEI (1999a)], are the winter isotherms of 10°C (corresponding to July in the southern hemisphere and to January in the northern hemisphere). This criterion is far from being perfect as Christophers showed (we will come back to the discussion of the geographical distribution and its relation with climate later in this work). The July 10°C isotherm is indicated in Figure (1) as a thick solid line [1].

Aedes aegypti has been reported, in the decade of the 1930s, in Bahía Blanca (on the Atlantic coast 38° 44', S 62° 16' W, average yearly temperature 15.4°C, July mean temperature 7.6°C) before the *Aedes aegypti* eradication program in the Americas, and is currently a permanent inhabitant of Buenos Aires city (34° 38' S, 58° 28' W, average yearly temperature 18.0°C, July mean temperature 11.0°C) [Schweigmann and Boffi (1998); de Garín et al. (2000); Carbajo et al. (2001)].

Historical records show that an epidemic of dengue in 1916 affected the cities of Concordia (31° 22' S, 58° 09' W, average yearly temperature 18.9°C, July mean temperature 12.3°C) and Paraná (31º44'S, 60º32'W, average yearly temperature 18.2°C, July mean temperature 11.2°C), and yellow fever epidemics decimated Buenos Aires city in 1852, 1857, 1870, 1871, 1896, 1899 and 1905. Nowadays, dengue is present in tropical regions of Argentina, i.e., in the northern provinces of Salta, Jujuy and Misiones [FUNCEI (1998, 1999b,a)].

In order to study the possible evolution of a dengue epidemic in any city

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[1] The temperature maps were produced by D R Legates and C J Willmott using terrestrial observations of shelter-height air temperature and shipboard measurements. The combined database of the world consisted of 17986 independent terrestrial station records and 6955 oceanic grid-point records. The data were interpolated to a 0.5° of latitude by 0.5° of longitude lattice. Most of the land station records are for the years between 1920 and 1980. Median air temperatures over the oceans are taken from the Comprehensive Ocean-Atmosphere Data Set (COADS) for the years 1950-79. COADS data are 2-degree latitude-longitude resolution. Legates and Willmott (1990).
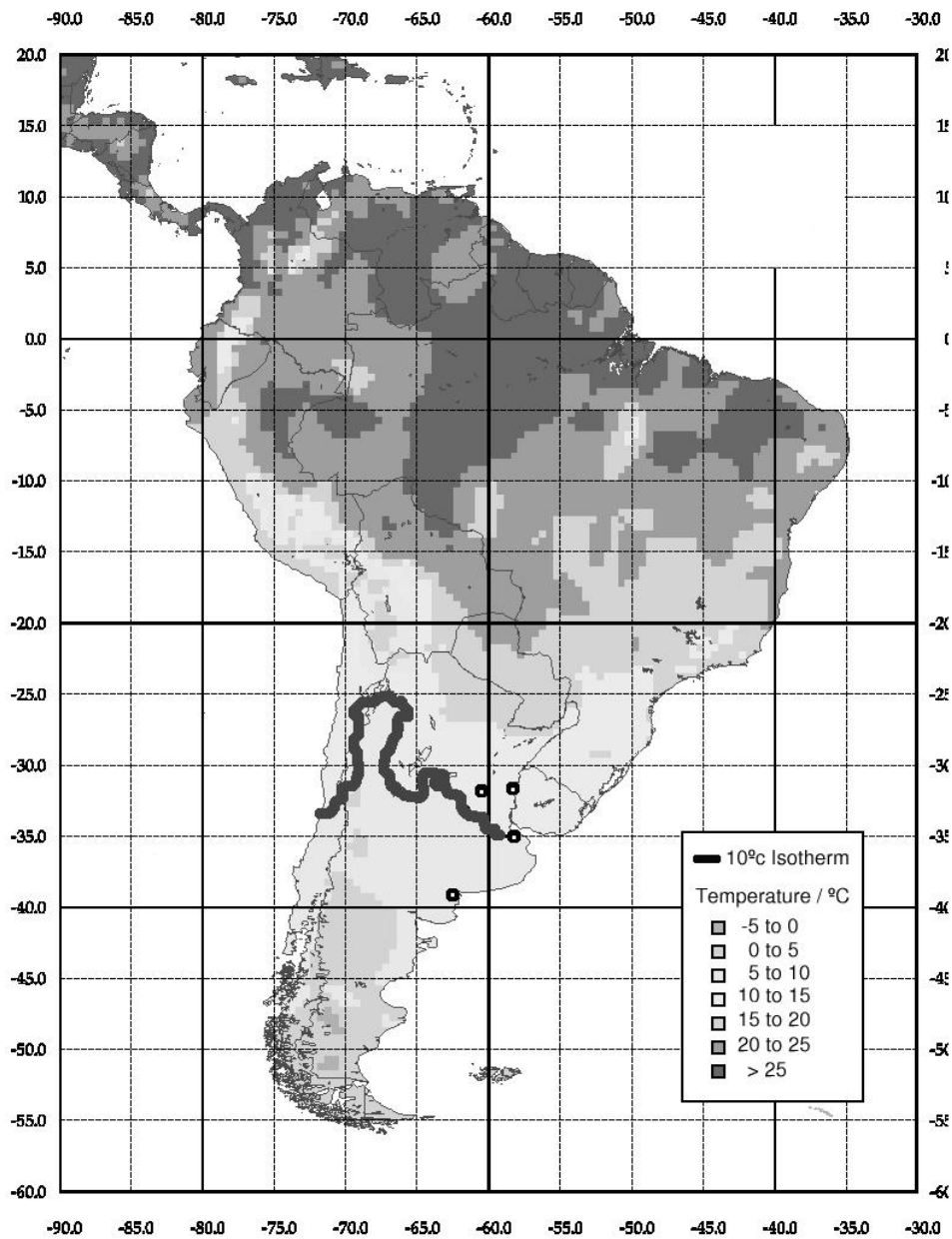
Fig. 1. July temperature in South America. The thick solid line represents the July 10°C isotherm. The cities of (South to North) Bahía Blanca, Buenos Aires, Paraná and Concordia are indicated on the map. Adapted from Legates and Willmott (1990).

with a temperate climate, such as Buenos Aires city, the seasonal variation of adult mosquito populations has to be taken into account since the abundance of adult females is the key factor for the transmission of the disease. Adult mosquitoes are close to extinction during the winter months and re-emerge in the spring. In contrast eggs are present all year long. The studies performed

in Buenos Aires [Carbajo et al. (2001)] suggest that extinctions of all forms of the mosquito as well as repopulation processes are common in localised areas of the city.

The *Aedes aegypti* eradication program carried out in Argentina (1954-1963), as part of the eradication program in the Americas was based on the use of insecticide (DDT) and the systematic destruction of breeding sites [Ministerio de Asistencia Social y Salud Publica (1964)]. As an application of the model we will be discussing how the number of available breeding sites affects the survival of the species.

The description of mosquito populations (as well as other insects) has been addressed using Dynamic Life Table Models [Focks et al. (1993a,b); Powell and Jenkis (2000); Depinay et al. (2004)]. These models are deterministic in nature and their stochasticity depends solely on the stochastic components of the climate data. Intrinsic stochasticity is not present and fixed rules are used in place of stochastic phenomena. For example, in [Focks et al. (1993a,b)] egg hatching cannot occur below an arbitrary temperature (an adjustable parameter, taken to be 22°C in the original work). However, experimental reports present several different minimal hatching temperatures varying from 20°C to 13°C [Christophers (1960)] (hatching of eggs at a temperature as low as 1°C has been reported, although the larvae were found dead). Indirect evidence of egg hatching below 17°C is provided by the observed sharp rise in the population of adults when the average daily temperature reaches approximately 18°C (field studies performed at Buenos Aires [Campos and Macia (1996)]). Reports of a sharp rise at 17°C in the northern city of Córdoba [Domínguez et al. (2000)] suggest that this value depends on additional factors and not only on the instantaneous temperature.

Moreover, Dynamic Life Table models are computationally demanding, preventing their use beyond homogeneous situations and do not allow for a simple mathematical analysis [Powell and Jenkis (2000)].

In the present work we develop a model for the evolution of *Aedes aegypti* as a (nonlinear or state dependent) Markov chain [Ethier and Kurtz (1986)] considering the four life stages of a mosquito: egg, larva, pupa and adult. For every life stage, the relevant changes are modelled in terms of random events with rates determined from the biological data available for *Aedes aegypti*. The rates depend on time through weather parameters. The relation with the deterministic models, emerging in the infinite populations limit, will also be addressed and their results compared with the stochastic model.

A minimalist stochastic model has several advantages over deterministic models. It shares much of the computational efficiency of models based upon differential equations but can deal properly with extinction processes. It is also

considerably less computationally demanding than following cohorts in dynamical table models and has the additional advantage that stochastic processes, such as development, are described in stochastic terms without resorting to additional (ad hoc) parameters to simulate them with deterministic methods. Additionally, the stochastic process has been approximated in this work with a Poisson method (see Appendix A) that represents a substantial saving of computer time compared to a direct Monte Carlo implementation of the stochastic process.

We will show in this work that the technical advantages allow for deeper scrutiny of the biological problem. In particular, they allow us to reconsider the habitat limits for *Aedes aegypti*.

In what follows we shall describe the basic biology of *Aedes aegypti* (Section 2), the formulation of the model (Section 3) and the evaluation of parameters based on the biological data (Section 4). Section 5 discusses the limitations of the model while Section 6 presents some results and issues of biological interest. The geographical limits for *Aedes aegypti* are discussed in Section 7 as a function of average yearly temperature, amplitude of the seasonal variation of the temperature and availability of breeding sites. The last section is dedicated to the summary, discussion and conclusions.

2 Biological notes on *Aedes aegypti*

The life cycle of a mosquito presents four distinct stages: egg, larva, pupa and adult (see Figure 2). In the case of *Aedes aegypti* the first three stages take place in or near water while air is the medium for the adult stage.

The eggs are laid on wet surfaces just above the water level (egg deposition). *Aedes aegypti* prefers small containers such as cans, buckets, flower pots, bottles, jars, urns and rain-water containers. Used car tires provide an ideal larval habitat and an adult resting site. In tropical climates larvae can also be found in natural cavities such as tree holes. The eggs of *Aedes aegypti* can resist desiccation and low temperatures for up to one year. Under the weather conditions considered in this work, desiccation is not a relevant mortality factor and has not been further considered. Although hatching of mature eggs may spontaneously occur at any time, it is greatly stimulated by flooding. Hence, hatching is more likely to occur after rainfall [Christophers (1960)].

The larva moult four times in a period of a few days (depending on the temperature) which culminates in the pupal stage (pupation). Both the larva and pupa are active stages, but only the larvae eat.
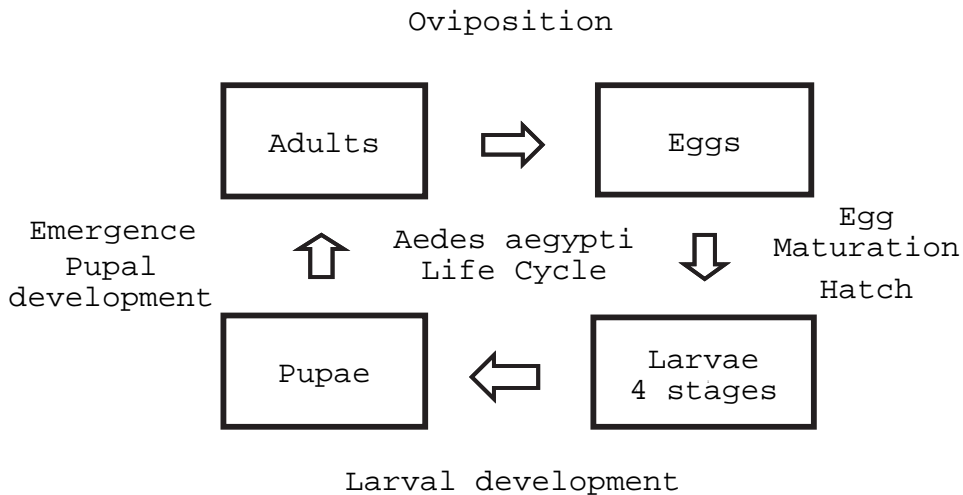
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┌─────────────┐              ┌─────────────┐
│             │     ──▷      │             │
│   Adults    │              │    Eggs     │
│             │              │             │
└─────────────┘              └─────────────┘
 Emergence          Aedes aegypti          Egg
 Pupal      ⇧       Life Cycle      ⇩    Maturation
development                               Hatch
┌─────────────┐              ┌─────────────┐
│             │              │             │
│    Pupae    │    ◁──       │   Larvae    │
│             │              │  4 stages   │
└─────────────┘              └─────────────┘
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Larval development

Fig. 2. Life cycle of *Aedes aegypti*

The pupal stage lasts from one day to a few weeks (depending on the temperature). At the end of the stage the adult emerges from the pupal skin (adult emergence).

The adult stage of the mosquito is considered to last an average of eleven days in the urban environment. Dengue and yellow fever are spread only by adult females. Mosquito females require blood to complete oogenesis. *Aedes* females are mainly anthropophagic, they prefer human blood to other mammals', although they can also bite other vertebrates. In this process, the female ingests human viruses with the blood meal. The viruses develop within the mosquito and are reinjected into the blood stream with the saliva of the mosquito in later blood meals.

Adult females lay an average of sixty-three eggs at each oviposition. The number changes according to the weight of the female and other factors. The gonotrophic cycle is regulated by the temperature and is longer for the first oviposition than for the subsequent ones [Christophers (1960)]. We will later distinguish between adult females in their first gonotrophic cycle, ($A1$ females), and in subsequent gonotrophic cycles ($A2$ females).

The natural regulation of *Aedes aegypti* populations has been discussed in some depth in the literature. In general terms, mosquito populations may display intra-specific competition for food and other resources within the same developmental cycle [Southwood et al. (1972); Dye (1982); Subra and Mouchet (1984); Gleiser et al. (2000)]. In the present work we will only consider competition within the larval stage, which is the only one well documented for *Aedes aegypti*. Predation may also be a factor in controlling the population of *Aedes aegypti* [Focks et al. (1993a)].

In practical terms many of these mechanisms may be indistinguishable, as

all of them will increase, in a first approximation, the mortality rate of the larvae as a function of larval density in the breeding site. In other words, each breeding site will be characterised by a carrying capacity.

Other mechanisms of population control have been reported for mosquitoes. In particular, inhibition of egg hatching due to a large density of larvae has been reported for *Ochlerotatus triseriatus* (formerly *Aedes triseriatus*) and may also affect *Aedes aegypti* populations[Livdahl et al. (1984)].

3   Mathematical model of the life cycle

The model considers five different populations: eggs (E), larvae (L), pupae (P), female adults not having laid eggs ($A1$), and female adults having laid eggs ($A2$). The population of adult male mosquitoes is not considered explicitly except that every time a female adult emerges, we will discount two pupae from the pool of pupae since about one half of the emerging adults are females. Actually, Arrivillaga and Barrera [Arrivillaga and Barrera (2004)] report a ratio of 1.02:1 male:female. Since we lack statistical information regarding oviposition, we will consider that each female lays a fixed number of eggs (63) at every oviposition.

The evolution of the five populations is affected by ten different possible events: death of eggs, egg hatching, death of larvae, pupation, death of pupae, adult emergence, death of young adults ($A1$), death of $A2$ adults, oviposition by $A1$ females and oviposition by $A2$ females. Table 1 summarises this information.

Events occur at rates that depend not only on population values but also on temperature, which in turn is a function of time since it changes over the course of the year. Hence, the dependence on the temperature introduces a time dependence in the event rates.

The inhibitory effect of larvae density on egg hatching, $\gamma(L)$, is modelled with a (negative) step function and its relevance will be later discussed in this work.

The evolution of the populations is modelled by a (state dependent) Poisson process [Ethier and Kurtz (1986); Andersson and Britton (2000)] where the probability of the state ($E, L, P, A1, A2$) evolves in time following a Kolmogorov forward equation (also known as master equation) that can be constructed directly from the information collected in Table 1.

The associated deterministic differential equation model [Kurtz (1970, 1971); Ethier and Kurtz (1986)] reads

	Event	Effect	Transition rate
1	Oviposition ($A1$)	$E \to E + egn$	
		$A1 \to A1 - 1$	
		$A2 \to A2 + 1$	$w_1(A1) = ovr1 * A1$
2	Oviposition ($A2$)	$E \to E + egn$	$w_2(A2) = ovr2 * A2$
3	Death of Eggs	$E \to E - 1$	$w_3(E) = me * E$
4	Egg hatching	$E \to E - 1$	
		$L \to L + 1$	$w_4(E, L) = elr(1 - \gamma(L)) * E$
5	Death of Larva	$L \to L - 1$	$w_5(L) = ml * L + \alpha * L(L - 1)$
6	Pupation	$L \to L - 1$	
		$P \to P + 1$	$w_6(L) = lpr * L$
7	Death of Pupa	$P \to P - 1$	$w_7(P) = (mp + (1 - ef) * par)P$
8	Adult emergence	$P \to P - 2$	
		$A1 \to A1 + 1$	$w_8(P) = par * ef * P/2$
9	Death Adults ($A1$)	$A1 \to A1 - 1$	$w_9(A1) = ma * A1$
10	Death Adults ($A2$)	$A2 \to A2 - 1$	$w_{10}(A2) = ma * A2$

Table 1

Event type, effects on the populations and transition rates for the developmental model. The coefficients are **ovr1, ovr2**: gonotrophic cycle coefficient (number of daily cycles) for adult females in stages 1 and 2.; **egn**: average number of eggs laid in an oviposition; **me**: mortality of eggs; **elr**: hatching rate; $\boldsymbol{\gamma(L)}$ hatching inhibition by larvae; **ml**: mortality of larvae; $\boldsymbol{\alpha}$: density-dependent mortality of larvae; **lpr**: pupation rate; **mp**: mortality of pupae; **par**: pupae into adults development coefficient; **ef**: emergence factor; **ma** : mortality of adults. All the coefficients depend on the temperature and hence present seasonal variations.

$$
\begin{aligned}
dE/dt &= egn * (ovr1 * A1 + ovr2 * A2) - me * E - elr * (1 - \gamma(L)) * E \\
dL/dt &= elr * (1 - \gamma(L)) * E - ml * L - \alpha * L^2 - lpr * L \\
dP/dt &= lpr * L - mp * P - par * P \\
dA1/dt &= par * ef * P/2 - ma * A1 - ovr1 * A1 \\
dA2/dt &= ovr1 * A1 - ma * A2
\end{aligned}
\tag{1}
$$

and is useful in the limit of infinite size homogeneous population with finite population density. Notice that in this limit we require $e = E/N, l = L/N, p = P/N, a1 = A1/N, a2 = A2/N$ to be finite, with N some large number, an ad hoc scale parameter to be identified later. The nonlinear mortality term for larvae becomes then $\alpha * L * (L - 1)/N$ and the limit exists provided $\alpha * N$ has finite limit. Then $\lim_{N \to \infty} (\alpha * N) L/N(L/N - 1/N) = l^2 \lim_{N \to \infty} (\alpha * N)$. The scale parameter has been restored to equation (1) while the correct dependency

with the continuous variables, that only emerge in the limit, has been kept for the nonlinear part of the larvae mortality. The parameter N will be identified in Section 4.3

4 Biological parameters

The rates of occurrence of the events described in Table 1 are specified in what follows for the case of *Aedes aegypti*. We will make several general simplifying hypotheses, which are justified for our application case but may require a revision in the general case. These hypotheses are: we will neglect the dependence on rainfall for the egg hatching rate, an assumption which is acceptable for regions where there is no dry season. We will also consider the mean daily temperature of breeding sites equal to the mean daily temperature of the air.

We shall make here the important distinction between breeding sites and water containers. While every breeding site is, by the biological nature of the mosquito, a water container, not every water container is a breeding site. For example, water containers with high exposure to the sun or in places infested by predators will not be effective as breeding sites and will not be considered as such in this work. We avoid in this form the accumulation of uncertainties produced by indirect calculations of breeding sites.

Since Buenos Aires is a city with temperate climate, we will neglect in this manuscript the often deadly effect of high temperatures. Adult *Aedes aegypti* seek cover under bushes and trees during hot weather and also choose their breeding sites in protected places. In temperate climates, containers under tree or bush protection reach temperatures substantially below the upper limits for development.

The different parameters appearing in the stochastic process described by Table 1 characterise *Aedes aegypti*. The stochastic population dynamic model makes no attempt to follow individual cohorts of mosquitoes but considers the full population as a homogeneous set. More detail could be incorporated into developmental stages in the four populations following more closely in this form the biology of the *Aedes aegypti*.

4.1 Developmental rates

There are four developmental rates in our model, and they correspond to egg hatching, pupation, adult emergence and gonotrophic cycle. Each of these rates is evaluated using the results of the thermodynamic model developed

Develop. Cycle (3)	$R_D(T)$	$R_D(298°K)$	ΔH_A	ΔH_H	$T_{1/2}$
Egg hatching	elr	0.24	10798	100000	14184
Larval develop.	lpr	0.2088	26018	55990	304.6
Pupal Develop.	par	0.384	14931	-472379	148
Gonotrophic c. ($A1$)	ovr1	0.216	15725	1756481	447.2
Gonotrophic c. ($A2$)	ovr2	0.372	15725	1756481	447.2

Table 2

Coefficients for the enzymatic model of maturation (equation (3)). R_D is measured in day^{-1}, enthalpies are measured in (cal / mol) and the temperature is measured in absolute (Kelvin) degrees.

by Sharp and DeMichele [Sharpe and DeMichele (1977)]. According to this model for poikilothermal development the maturation process is controlled by one enzyme which is active in a given temperature range, the enzyme is deactivated at low, T_L, and high, T_H, temperatures. The development is stochastic in nature and is controlled by a Poisson process with rate $R_D(T)$. In general terms $R_D(T)$ takes the form

$$R_D(T) = R_D(298°K) \times \qquad\qquad\qquad\qquad\qquad\qquad (2)$$
$$\frac{(T/298°K)\exp((\Delta H_A/R)(1/298°K - 1/T)}{1 + \exp((\Delta H_H/R)(1/T_H - 1/T)) + \exp((\Delta H_L/R)(1/T_L - 1/T))}$$

Here T_H, T_L are absolute temperatures (°Kelvin) while ΔH_A, ΔH_H and ΔH_L are thermodynamic enthalpies characteristic of the organism, in particular, ΔH_L is negative in general while ΔH_H is positive. R is the universal gas constant.

Schoofield et al. introduced a simplified model with only high temperature deactivation [Schoofield et al. (1981)]. The model reads

$$R_D(T) = R_D(298°K)\frac{(T/298°K)*\exp((\Delta H_A/R)(1/298°K - 1/T))}{1 + \exp(\Delta H_H/R)(1/T_{1/2} - 1/T))} \quad (3)$$

where $T_{1/2}$ is the temperature when half of the enzyme is deactivated because of high temperature. We adopt Schoofield's model since it is flexible enough for fitting the available biological data.

In Table 2 we present the values for the different coefficients involved in the events: egg hatching, pupation, adult emergence and gonotrophic cycle. The values are taken from [Focks et al. (1993a)]. We will later discuss this particular application of the enzymatic model.
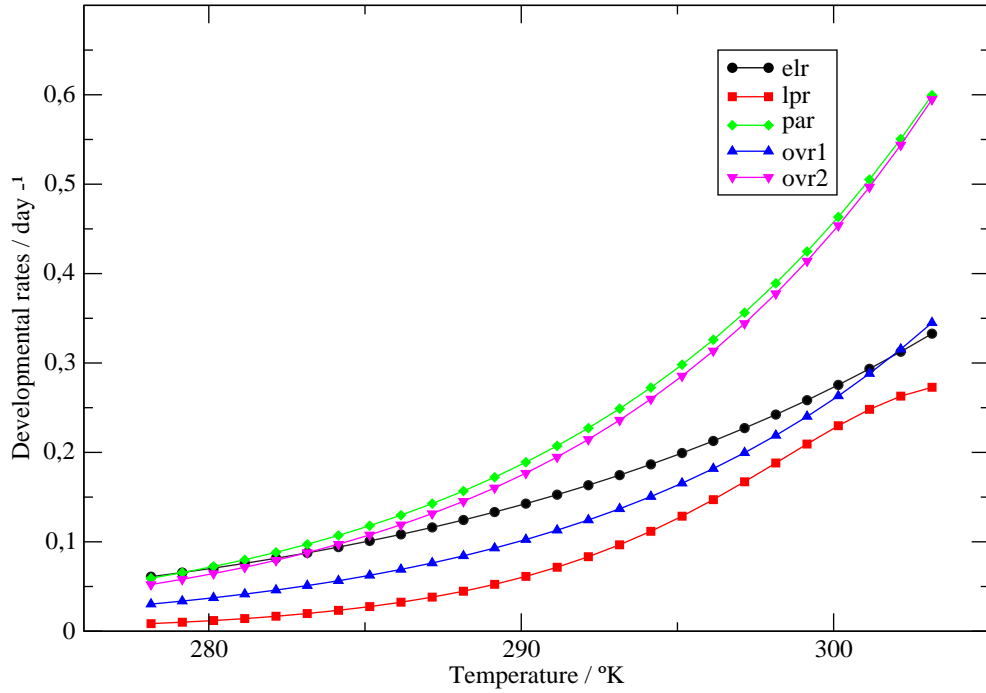
Fig. 3. Developmental rates according to Table 2 as a function of the temperature. **elr**: hatching rate; **lpr**: pupation rate; **par**: pupae into adults development coefficient; **ovr1**, **ovr2**: gonotrophic cycle coefficient (number of daily cycles) for adult females in stages 1 and 2.;

The resulting developmental rates are displayed in Figure 3 as a function of temperature.

4.2 Mortality, emergence and oviposition rates

The different mortality rates as well as the emergence rate and average deposition rate have been taken from [Focks et al. (1993a); Christophers (1960)] and are as follows.

Oviposition Females lay a number of eggs that is roughly proportional to their body weight ($46.5 eggs/mg$) [Bar-Zeev (1957); Nayar and Sauerman (1975)]. The mean weight of a three-day-old female is $1.35 mg$ [Christophers (1960)], hence we estimate the average number of eggs laid in one oviposition as **egn** $= 63$. The gonotrophic cycle for the first oviposition takes longer than in subsequent ovipositions, a fact reflected in the parameters of Table 2. The number of ovipositions for an adult female estimated from the parameters of the model are: one at $20°C$, four or five at $25°C$ and six at $30°C$.

11

Egg mortality   The mortality of the eggs is chosen to be $\mathbf{me} = 0.011/day$ and is independent of the temperature in the range $278°K \leq T \leq 303°K$ [Trpis (1972)].

Larva mortality   The death of the larvae is divided in two contributions as explained above. One contribution accounts for natural mortality under optimal conditions and depends only on the temperature. Its rate is approximated by $\mathbf{ml} = 0.01 + 0.9725 \exp(-(T-278)/2.7035)$ and is valid in the range $278°K \leq T \leq 303°K$. [Horsfall (1955); Bar-Zeev (1958); Rueda et al. (1990)]. The other contribution is the density-dependent (regulatory) mortality, due to the accumulation of adverse factors. This contribution will be considered separately in the next subsection.

Death of Pupae   The intrinsic mortality of a pupa has been considered as $\mathbf{mp} = 0.01 + 0.9725 exp(-(T-278)/2.7035)$ [Horsfall (1955); Bar-Zeev (1958); Rueda et al. (1990)].

Emergence   Besides the daily mortality in the pupal stage, there is an important additional mortality associated with the sometimes unsuccessful emergence of the adult individual. We assume a mortality of 17% of the pupae at this event, which is added to the mortality rate of pupae. Some 83% of the pupae that reach maturation will emerge as adult mosquitoes, hence the emergence factor is $\mathbf{ef} = 0.83$ and multiplies the developmental rate of the pupa already described [Southwood et al. (1972)].

Adult death   The mortality of adults is taken to be independent of the temperature. The mortality rate for an adult is $\mathbf{ma} = 0.091/day$ in the range $278°K \leq T \leq 303°K$ [Horsfall (1955); Christophers (1960); Fay (1964)].

4.3   State-dependent rates

From a mathematical point of view, state dependent rates (also called density-dependent rates in the mathematical literature) introduce the necessary non-linearities that prevent an exponential growth (on average) of the populations. Density-dependent transition probabilities reflect the regulatory processes that affect the populations.

We have introduced two regulatory process: density-dependent mortality of larvae and egg-hatching inhibition by larvae.

Density-dependent mortality of larvae This regulatory mechanism may be due to several concurrent processes such as food limitations, chemical interactions, presence of specialised predators at the breeding site, and more. It reflects not only a characteristic of the species but also a characteristic of the environment. As such, it is expected to take different values at different locations.

Crowding effects for larvae have been reported for *Aedes aegypti* [Dye (1982)]. Other *Aedes* mosquitoes such as *Aedes albopictus* are more exposed to predation as a consequence of being able to use breeding sites in the wilderness.

Predation is believed to be an important factor in the control of *Aedes aegypti* in South America where *Aedes aegypti* is a domestic mosquito unable to survive in unprotected places such as large parks. *Aedes aegypti* can live in the wilderness at other locations such as in North America and Central America.

In the present work this effect is taken into account as the simplest nonlinear correction to the larvae mortality, i.e.:

$$\omega_5(L) = mlL + \alpha L(L-1) \tag{4}$$

the value of α can be further decomposed as

$$\alpha = \alpha_0/BS \tag{5}$$

with α_0 being associated with the carrying capacity of a single (standardised) breeding site and BS being the number of breeding sites grouped as a single-site-equivalent in the homogeneous model. The value of α_0 can be fitted to observed values in the region being simulated. Recalling the deterministic model (1), the requirement for αN to have a finite limit when N goes to infinity can be rephrased as $\lim_{N \to \infty} N/BS = 1$. In this way BS becomes the internal parameter of the stochastic model that controls the approximation to the deterministic model for population fractions. In the deterministic model BS will only be a scale parameter.

Hatching inhibition by larvae The possibility of a complex regulatory process, in which the high density of larvae inhibits egg hatching, inducing the eggs to enter diapause, was unearthed by Livdahl [Livdahl et al. (1984)]. We have introduced this effect through a factor lowering the hatching rate when the larvae exceed a predetermined density. The hatching rate becomes then

$$w_4(L) = \mathbf{elr}(1 - \gamma(L)) \tag{6}$$

13

with

$$\gamma(L) = \begin{cases} 0 & \text{if } L/BS < a_0 \\ 0.63 & if \ L/BS \geq a_0 \end{cases} \tag{7}$$

where a_0 is the critical value resulting from the product of the critical density times the estimated average volume of the breeding sites.

According to Livdahl et al. (1984) the hatching fraction changes somewhere between 10 and 70 larvae per litre. The region between these values has not been explored, hence we have considered that the inhibition effect takes place for densities above a given value named the critical density. Critical density values between 10 and 70 larvae per litre have been considered as well as an average size of the breeding site of 1/2 litre.

5   Discussion of the biological model

As in any phenomenological model, there are several compromises that have to be addressed. They emerge between the precision of the description and the analytical, as well as numerical, difficulties introduced.

The philosophy of our model is minimalist, i.e., we have attempted to produce the simplest model for the dynamics of *Aedes aegypti* populations compatible with existent data. It may be later necessary to introduce age structure (for example, introducing the different instars in larvae development), adult male populations or other details in the description. It may also be necessary to improve the weather data incorporating humidity and rainfall for example.

The incorporation of the spatial extension of the model seems to be the most urgent need. Dispersal strategies of mosquitoes might be a determining factor in their survival in temperate climates as well as in environments with a low density of breeding sites.

A second source of deficiencies of the model has its origin in the quality of the biological data we have been able to collect.

Measurements of developmental rates at temperatures in a range larger than $278°K - 303°K$ are needed if the parameters of the enzymatic model are going to be retrieved in a realistic form. The parameters listed in Table 2 make little biological sense in several cases. Temperatures as high as $14184°K$ or as low as $148°K$ as well as negative deactivation enthalpies (ruled out by hypothesis in the model) are easily explained as artifacts of a nonlinear fit based on

data within a range insufficient to display the behaviour associated with the enzymatic model. Actually, it is possible to fit the same data with equivalent accuracy with a substantially smaller number of parameters.

Statistics for egg deposition would also help to improve the quality of the model by removing the hypothesis of a fixed number of eggs laid by deposition. Notice that egg deposition is influenced by environmental variables since it depends on body weight of the females which, in turn, depends on feeding conditions in the larval stage. Arrivillaga and Barrera [Arrivillaga and Barrera (2004)] report body weights of females from 0.554mg to 2.338mg under laboratory conditions, however, females collected in field studies in tropical Venezuela show different weights at different seasons with weight averages from 0.74 to 0.94 mg.

The inhibitory effect produced by larval population density on egg hatching reported in Livdahl et al. (1984) presents hatching fractions for low densities and for high densities while there are no measurements in the density range 10-70 larvae per litre where the transition from low to high density occurs. Hence, there is room for improving the description of the inhibitory effect.

Other effects regulating the dynamics of the population such as inhibition of oviposition in larvae saturated breeding sites may be also in action but very little is known about them, and their present status is closer to "conjecture" than to anything else.

The effects of food deprivation and starvation of larvae have not been explicitly incorporated in the model although they might be a relevant mechanism for the regulation of the mosquito populations [Arrivillaga and Barrera (2004)].

6 Results

6.1 Analysis of the deterministic model

We shall explore the elementary solutions of the deterministic model (1) using standard methods of nonlinear analysis (Wiggins (1990); Solari et al. (1996)).

The fixed points of (1) satisfy

$$E_0 = L_0 \frac{egn * (ovr2 + ma) * ovr1 * par * ef * lpr}{2 * ma * (me + elr * \mu)(mp * ma + mp * ovr1 + par * ma + ovr1 * par)}$$
$$P_0 = L_0 \frac{lpr}{mp + par}$$

15

$$A1_0 = L_0 \frac{par * ef * lpr}{2 * (mp * ma + mp * ovr1 + par * ma + ovr1 * par)}$$

$$A2_0 = L_0 \frac{ovr1 * par * ef * lpr}{2 * ma * (mp * ma + mp * ovr1 + par * ma + ovr1 * par)}$$

$$0 = elr * \mu * E_0 - ml * L_0 - \alpha * L_0^2 - lpr * L_0 \qquad (8)$$

with $\mu = 1 - \gamma(L_0)$.

There are at most three solutions of (8). The trivial state, with all the populations zero and two non trivial solutions, one corresponding to $\gamma(L_0) = 0$ and the second one corresponding to $\gamma(L_0) \neq 0$ (in both cases they are the root of a homogeneous polynomial of order two).

The non trivial solutions are biologically significant only when the populations are positive, a condition that is written as

$$L_0 * \alpha = elr * \mu \left(\frac{E_0}{L_0} \right) - (lpr + ml) \geq 0 \qquad (9)$$

where equality in the last term corresponds to the condition for the transcritical bifurcation that signals, in parameter space, the point at which the population is viable under constant temperature conditions. This case corresponds to considering $\mu = 1$ since the density of larvae is zero. The bifurcation occurs, using the parameter values given in the previous sections, at $10 \leq T \leq 10.5°C$.

We further notice that the equilibrium point is always proportional to $1/\alpha$ and by (5) it is proportional to BS/α_0, i.e., the environmental variable BS determines the size of the equilibrium population in the deterministic model (to obtain the result, notice that $\gamma(L)$ depends only on the quotient L/BS in (7)). Further notice that the occurrence of BS in (1) can be suppressed by a change of scale, rescaling all the population variables by $1/BS$. Hence, the occurrence of BS in (1) is somewhat artificial, the deterministic model is actually a model for population densities (Kurtz (1971)).

It is important to realize, at this point in the discussion, that the condition for the bifurcation is independent of the number of breeding sites, BS. This result is expected since the deterministic equations are, in essence, equations for the variables $(A1, A2, E, L, P)/BS$ valid in the limit $BS \to \infty$ with $\|(A1, A2, E, L, P)/BS\|$ finite (Ethier and Kurtz (1986)), such a population has an indefinitely large number of available breeding sites.

The third solution of (8) is not associated with a bifurcation since the function $\gamma(L)$ is not smooth. We will not discuss it further since the discussion does not carry significant contributions to the understanding of the biological problem.
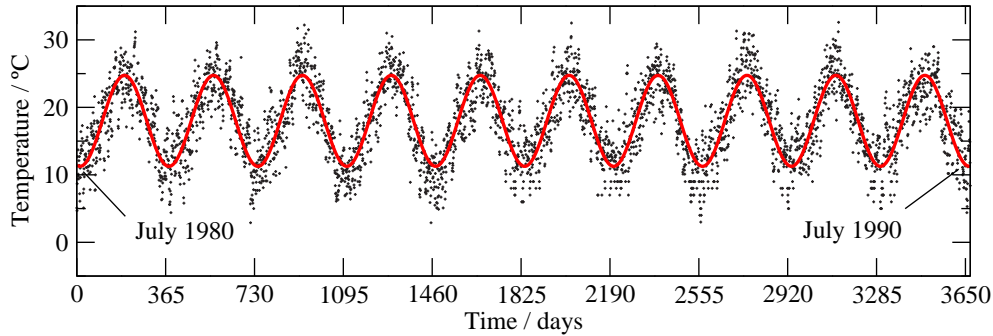
Fig. 4. Fit of Buenos Aires mean daily temperatures using equation (10). The data corresponds to Ezeiza (Buenos Aires airport) station of the Servicio Meteorológico Nacional, Argentina.

6.2 Seasonal variation

The discussion of the viability of the mosquito under constant weather conditions is relevant only for laboratory studies, but in any urban area the mosquito will be subject to seasonal changes in the temperature. In what follows we have adopted a simple model for mean daily temperature variation that contains only the deterministic component of the temperatures. The model is taken after [Király and Jánosi (2002)] and takes the form:

$$T = a + b\cos(\frac{2\pi t}{365.25 days} + c)$$ (10)

with the time measured in days beginning on the first of July. The values for the parameters a, b and c fitted from temperature records in the period 1980-1990 (when *Aedes aegypti* reappeared in Buenos Aires) are: $a = 18.0°C$; $b = 6.7°C$ and $c = 9.2$. The temperature variation during the day has not been taken into account in the model, keeping the model simple. This simplification is not expected to introduce important distortions in the population dynamics (Focks et al. (1993a); de Garín et al. (2000)) at this level of the description since the characteristic times of all the processes involved are of several days and their probabilities are ruled by time-integrals of the rates. Hourly temperature fluctuations are then smoothed by the dynamics.

The adjusted parameters for the observations corresponding to Buenos Aires city (Ezeiza station of the Servicio Meteorológico Nacional, Argentina) are presented in Figure 4, for which the fit was performed using a Levenberg-Marquardt algorithm.

17

6.3 Deterministic stability analysis of the trivial solution

Once again, the viability of the mosquito population corresponds to the loss of stability of the trivial solution (absence of the mosquito). The stability analysis using Floquet's method requires finding the monodromy matrix after a one year period. Notice once again that the transition rates in (1) depend indirectly on time because of their dependence on the temperature which by (10) is periodic.

The equation for the monodromy matrix around the trivial fixed point reads:

$$
\frac{d\mathbf{M}}{dt} =
\begin{pmatrix}
-elr - me & 0 & 0 & egn*ovr1 & egn*ovr2 \\
elr & -ml - lpr & 0 & 0 & 0 \\
0 & lpr & -(mp + par) & 0 & 0 \\
0 & 0 & par*ef/2 & -ma & ovr1 \\
0 & 0 & 0 & ovr1 & -ma
\end{pmatrix} \mathbf{M}
\tag{11}
$$

with the initial condition $\mathbf{M}(0)$ being the identity matrix.

The extinction solution is stable when all the eigenvalues of the monodromy matrix $\mathbf{M}(1year)$ are less than one in modulus. When the first eigenvalue crosses the unit circle the extinction solution loses stability and a (stable) periodic solution emerges in a transcritical bifurcation. The bifurcation set obtained numerically is presented in Figure 8 (solid green curve). Technical details on the application of stability theory to the present case are presented in Appendix B.

6.4 Numerical explorations of the stochastic model

Simulations for the homogeneous model (1) were carried out using the Poisson Approximation for fixed time intervals [Solari and Natiello (2003b,a)] (see Appendix A).

The characteristic volume of a breeding site was estimated to be about half a litre and an average of 7 larvae per breeding site are found during the most favourable week of the year.

The time evolution of the population was considered with initial conditions in the winter time, when all the subpopulations are presumably extinct or near
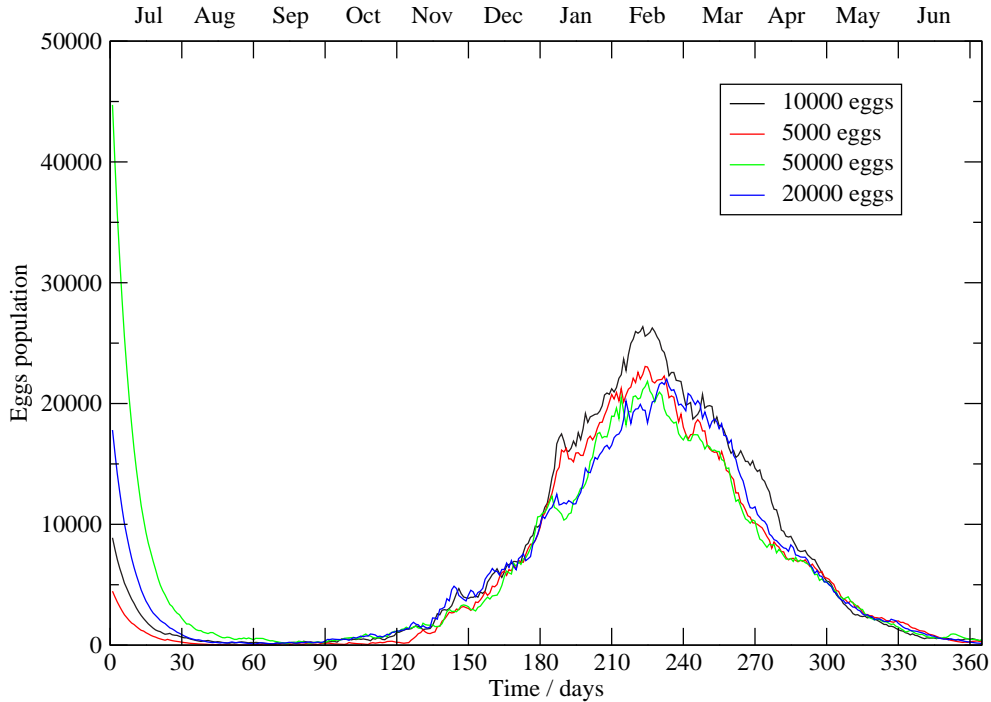
Fig. 5. Dependence of the egg population with initial value. Different values for the egg subpopulation were arbitrarily specified at the coldest day of the winter. The populations presented no observable sensitivity to the initial conditions when the next favourable cycle (spring-summer) developed. The example corresponds to the egg population for $BS = 50$.

extinction except the subpopulation of eggs.

Runs with different initial values presented no significant differences in any population numbers provided the mosquito survived until the following (spring-summer) favourable season (see Figure 5). These results show a strong regulatory capability of the environment. The carrying capacity of the environment, as reflected by the parameter BS, regulates the mosquito populations which, additionally, show little to no memory of the population situation one year before. It could be said in this regard that the reproductive potential of *Aedes aegypti* promotes the populations found at the beginning of the favourable period (spring) up to the limits set by the environment.

6.5 Biological checkpoints

The homogeneous model introduces a representation of the individual biological processes involved in the life cycle of *Aedes aegypti*. It also allows for the calculation of some observed quantities not used in the construction of the model.
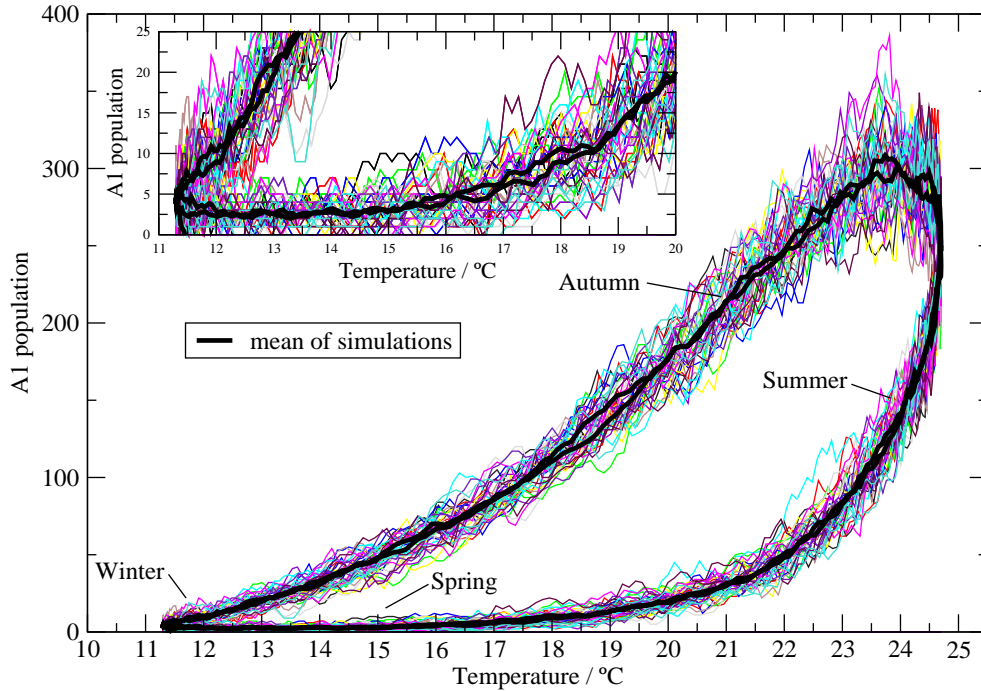
Fig. 6. Adult mosquito populations plotted against the temperature for 150 breeding sites for two years. The wide line represents the average of one hundred individual realizations.

Under regulated (constant) laboratory conditions *Aedes aegypti* is able to persist above 10°C [Christophers (1960)]. According to the results of the present model the minimal temperature lies between 10° and 10.5°C provided an infinite number of breeding sites are available (results based on the deterministic model).

In temperate Buenos Aires, the population density of adult *Aedes aegypti* exhibits a sharp rise during the spring time (6). The rise depends on the temperature as well as population variables. According to a field study [Campos and Macia (1996)] the effective emergence of adults is observed at 18°C. Simulations made with 150 breeding sites/ha (corresponding to the largest density of breeding sites found in Buenos Aires) suggest that the population of adult mosquitoes begins to increase almost monotonically when the temperature is between 15° and 19°C (see figure 6) depending on random factors. This temperature is roughly independent of the number of breeding sites provided there are enough to avoid the extinction of the mosquito during the winter time. Hence the observed temperature is compatible with the range predicted by the model. The temperature for the effective emergence of adults depends not only on the biology of the mosquito but also on the temperature patterns of the environment and is expected to change from city to city. It is important to realize that this effective emergence temperature was not directly included in the model and is not associated with any particular parameter.

20

The cycle of the mosquito follows the temperature with some delay (see Figure 6). The adult population reaches its minimum after the coldest days of the year, the reproductive season is then triggered by the temperature and the population number reaches a maximum (controlled by the carrying capacity of the environment) after the hottest days of the year.

7 Extinction/survival thresholds

What is the world wide potential habitat for *Aedes aegypti*? What percentage of breeding sites has to be destroyed to eradicate the mosquito from a given city? These two questions might appear, in a first inspection, unrelated but we will show they are closely related.

Christophers considered the first question [Christophers (1960)]. Given the fact that *Aedes aegypti* cannot proliferate (develop) under laboratory experiments at temperatures below 10°C, it was then argued that, if mosquitoes were to survive the winter in larval or adult form, the 10°C winter (July in the South or January in the North) isotherm would then give an idea of their potential habitat. Notice that with the temperature profile adopted in equation (10) the average July temperature results from averaging the temperature profile during the 31 days of the month of July, resulting in $T_{July} = a - b\,0.98732$, hence Christopher's criterion is represented by $a = 10°C + b\,0.98732$ (Christophers' criterion is illustrated in Figure 8 -straight line-).

A serious problem with Christophers' criterion is that the hypothesis of larva or adult winter survival does not hold. Mosquitoes can survive the winter in the egg form as it is verified in Buenos Aires [Schuster (1984)]. Christophers realized that there were abundant exceptions to his criterion, he mentioned in particular the case of Bahía Blanca (South America) as well as records of the presence of the mosquito at several cities on the East coast of North America (the northernmost one being Boston) as well as many other cities around the world.

The importance and relevance of egg winter survival was advanced *before* Christophers' criterion by Carter [Carter (1931)] where the occurrence of *Aedes aegypti* in ports is discussed in the following terms:

If breeding places were available and the temperature on landing high enough for the full functional activity of the insects, a colony could be established and would be permanent or not, according to the winter temperature of the locality, and the colony would last until the species (eggs) were destroyed by the cold, which might be the first winter; or, in border-line places, the species might live several years, to be destroyed eventually by

some winter of unusual length or severity. Such seems to have been the case in Philadelphia and possibly New York in the latter part of the eighteenth century.

Carter's survival criterion (based on egg winter survival) acknowledges not only winter temperature as a factor but also the duration of the winter. We will show in section 7 that our simulations are fully compatible with Carter's considerations.

If the potential habitat of the mosquito is going to be discussed, some additional specifications are needed. We will consider in this section the influence of the temperature in terms of average yearly temperature and the seasonal amplitude as presented in equation (10). We will also specify different environmental conditions represented by different values of the parameter BS. Additionally, we will see that the deterministic limit is achieved for unrealistically large numbers of breeding sites.

By a continuity argument, the transition between a region where the mosquitoes can live permanently and another region where they cannot live at all must be mediated by a transition region where both the presence of the mosquito for several years and its extinction are likely to occur. The definition of this region has a certain degree of arbitrariness. After all, the Markov process describing the problem has the extinction state as an absorbing one.

We arbitrarily defined a region to be at the border of the potential habitat when an already established population (i.e., a population that has survived at least one year in the habitat) has a survival probability for the next year of 1/2. A system with parameter values satisfying this condition will be said to be at threshold. In Figure 7 we show the dependence of the next year survival probability as a function of average yearly temperature. The transition from 0.99 to 0.01 probability takes place with an approximate change from 20.8°C to 14.5°C in the average temperature for a seasonal amplitude of 6.7°C considering 50 breeding sites (see Figure 7).

The threshold is then a hypersurface in parameter space, in our case a curve relating the values of the parameters a, b in equation (10) controlling the temperature and the number of breeding sites assigned to the homogeneous region.

For infinitely many breeding sites available, the threshold corresponds to the lost of stability of the extinction solution in the deterministic model (1). The deterministic threshold begins at around 10.5°C when there are no seasonal variations and is lower for higher seasonal variations (see figure 8).

Infinitely many available breeding sites are, clearly, unrealistic. We tentatively estimated the extinction thresholds for a homogeneous place having a number
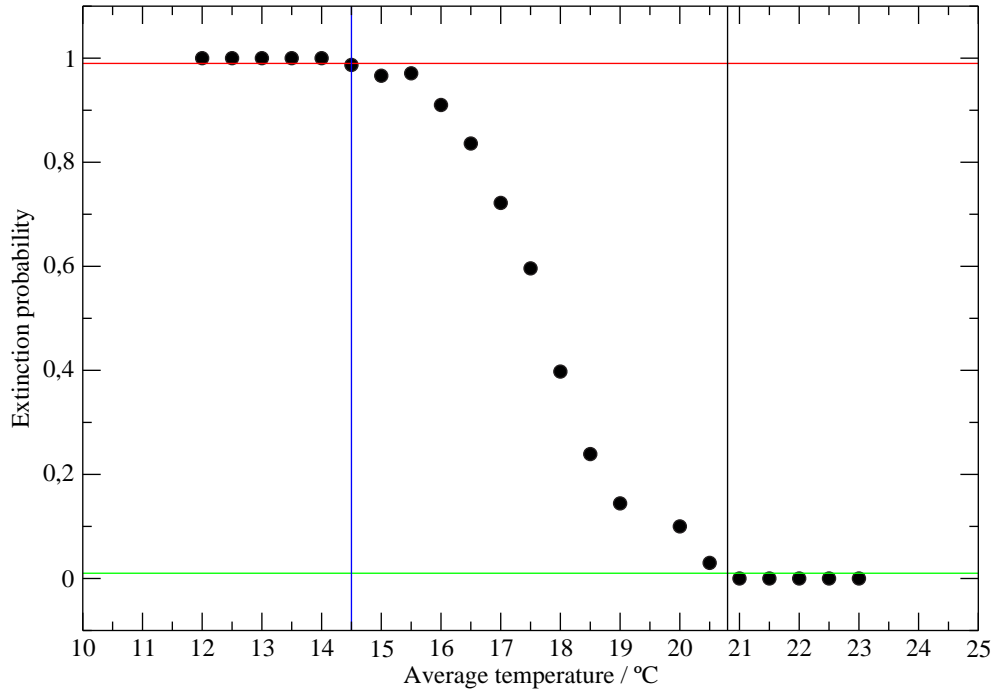
Fig. 7. Probability for the next year extinction as a function of average yearly temperature. The thermal amplitude is 6.7°C and the number of breeding sites is $BS = 50$. The probabilities were estimated as the number of extinctions in 200 simulations.

of breeding sites between the highest ($BS = 150$) and the lowest number of breeding sites ($BS = 15$) found in a $(100\text{m})^2$ patch in field studies at Buenos Aires. Also displayed in Figure 8 are calculations performed for unrealistically large number of breeding sites for illustrative purposes.

The parameter α_0 in equation (5) was fitted to reproduce the number of larvae per breeding site found during the most favourable week of the year (in terms of number of larvae) in field studies performed at Buenos Aires cemeteries [Vezzani et al. (2004)] and was given the value $\alpha_0 = 1.5$. Since α_0 is the only adjustable parameter of the model, we produced simulations with various choices of α_0 under the conditions corresponding to cemeteries in Buenos Aires, adjusting the α_0 value to match the average number of larvae per breeding site during the summer week with the largest number of larvae. This value is only a rough estimation, and it is not worth refining the value of this parameter considering the accuracy of the available data. Each container was considered to have an average of half a litre of water producing an estimated 14 larvae per litre (7 larvae per half litre breeding site), a number that is relevant only when considering egg hatching inhibition.

The results of the simulations are displayed in Figure 8 (dots). Notice that the stochastic thresholds show an average temperature higher than in the deterministic case as one would have expected, but also, that an increase in the
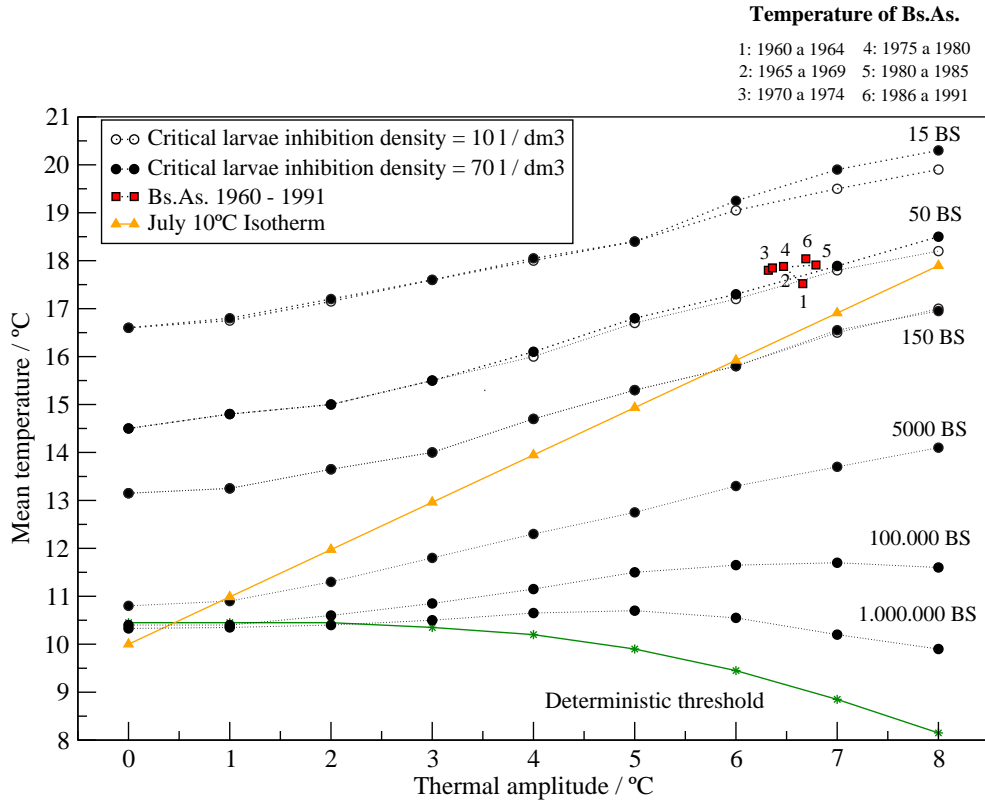
23

Fig. 8. Threshold parameters for the *Aedes aegypti* populations in the parameter space (Mean temperature, Thermal amplitude), i.e., parameters (a, b) of equation (10). The points correspond to estimations using the stochastic model for several different carrying capacities of the environment. Dotted lines are a guide for the eye relating points corresponding to the same number of breeding sites. The straight line corresponds to Christophers' criterion, while the curved line corresponds to unlimited resources (deterministic model).

thermal amplitude (seasonal variation) renders the settlement of *Aedes aegypti* more difficult. Figure 8 also shows the temperature values corresponding to Buenos Aires city in the period 1960-1991 (squares), a period of time that includes the end of the eradication program as well as the years of the reinfestation. It is interesting to notice that with the highest values for BS the populations can survive even in isolation, however, with the lower values local extinctions are expected, hence emphasising the roles as reservoirs of places with high density of breeding sites.

There are different aspects of Figure 8 worth mentioning. On the mathematical side, the slow convergence of the stochastic results towards the deterministic curve is noticeable. As many as 10^6 breeding sites are needed to get close to it, a number sharply contrasting the estimation of no more than 150 breeding sites within a $(100m)^2$ patch.

On the biological side it is interesting to notice that, for relatively high seasonal

24

thermal amplitude, the effects of the favourable weather are less relevant than the effects of the not favourable weather, i.e., higher average yearly temperatures are required for higher amplitudes. Actually, the population is regulated in spring-summer by the environment and its carrying capacity. Even when the weather is more favourable, the mosquito populations cannot increase because of the saturation of the breeding sites. Hence, egg populations at the beginning of the winter are expected to be roughly independent of the high temperatures of the summer.

The mosquito spends parts of the winter in the egg stage suffering a daily mortality of eggs, which is roughly independent of the temperature. It is then the duration of the unfavourable period that makes a difference for the survival of the mosquito population. Hence, the mortality increases with the thermal amplitude (for the same average temperature). The lines of equal unfavourable (winter) time are straight lines with positive slopes in Figure 8 (not shown) and this is the apparent form that the threshold curves take for large amplitudes.

The biology encoded in the model is then fully compatible with the qualitative discussion given in [Carter (1931)].

According to the present results, a map of South America with the cities likely to support domestic populations of *Aedes aegypti* can roughly be based on the 15°C isotherm (yearly average). This criterion corresponds to the average yearly temperature of the threshold with seasonal amplitudes and maximum number of breeding sites as those found in Buenos Aires.

Of the 661 towns and cities of Argentina with present or historical records of *Aedes aegypti* populations, we have displayed on the map of average yearly temperatures those lying below the July 10°C isotherm (data extracted from [Morales et al. (2004)]). Notice that the 15°C average yearly temperature isotherm gives a reasonable idea of the habitat limits for *Aedes Aegypti*.

7.1   Egg hatching inhibition

The effects of egg hatching inhibition by high larvae density on the threshold are minimal in this study. We repeated the threshold calculations changing the critical density (7) from 10 to 70 larvae per litre. The resulting threshold values are almost identical, with the threshold slightly lower in mean temperature for the lower critical density. This result was in part expected since egg-hatching inhibition by larvae will produce a higher reserve of eggs for the winter period and then, a larger probability of surviving the unfavourable season. However, in the environmental conditions considered, the effect is only evident in the peak of the breeding season and most of the produced eggs will not reach the larva stage (see Figure 10).
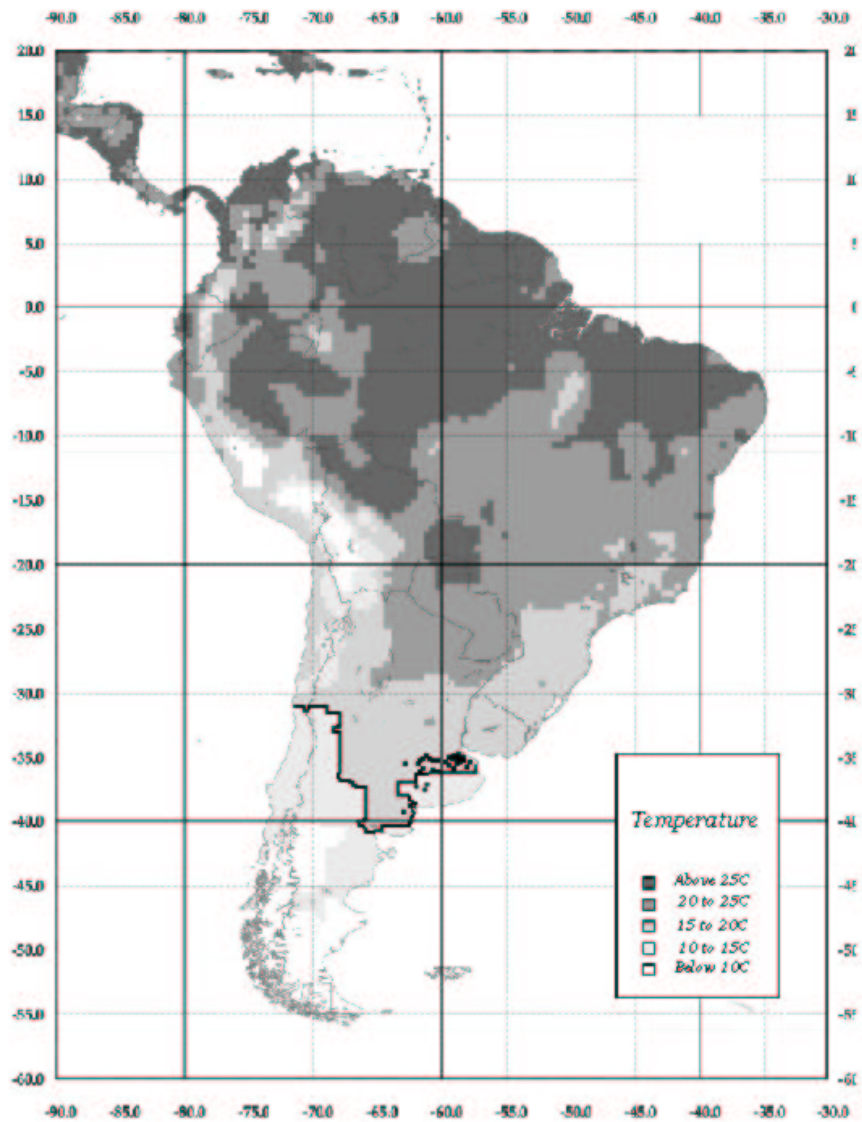
Fig. 9. Average temperature (yearly) in South America. Dark grey for regions with average temperature above 25°C, grey for temperatures between 20 and 25°C, light grey for temperatures between 15°C and 20°C and white for temperatures lower than 10°C. The dots represent towns and cities of Argentina below the 10°C July isotherm where the mosquito has been detected. The black contour line represents the 15°C average yearly isotherm.
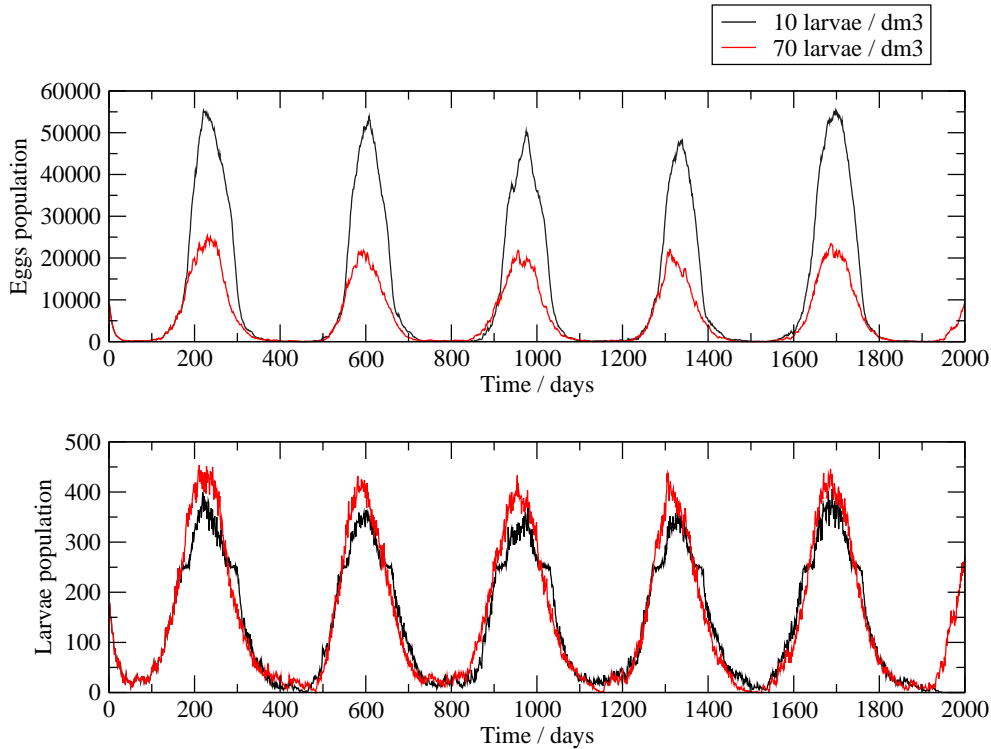
Fig. 10. Differences in egg and larva populations for the two extreme values of the egg hatching inhibition effect, simulated for 50 breeding sites. The shoulders in the population data are an artifact of the step function (7) used to simulate the effect in the absence of better experimental data determining the function.

7.2 *Extinction probabilities as a function of initial conditions*

As another example of the information that the model can provide, we studied the changes in the probability of extinction during the first year as a function of the number of eggs remaining in the winter. The study is motivated by a possible strategy against the mosquito that consists of removing as many eggs as possible in the winter time, thereby trying to drive the population into extinction.

We considered the case of $150BS$ in Buenos Aires climate and produced extinction statistics based on 1000 runs for each initial condition. All runs began the coldest day of the year with a population consisting only of eggs.

The results of the simulations are presented in Figure 11. Two solid lines have been drawn in the plot. The first one connects the results for initial number of eggs below 100 and is a straight line in the logarithmic scale of the plot. It clearly represents the fate of small numbers of eggs and is accounted for the probability of one egg (or its biological evolution) to die. The processes are independent when the population is small (where "small" is relative to the carrying capacity of the patch) and hence, the exponential dependence with
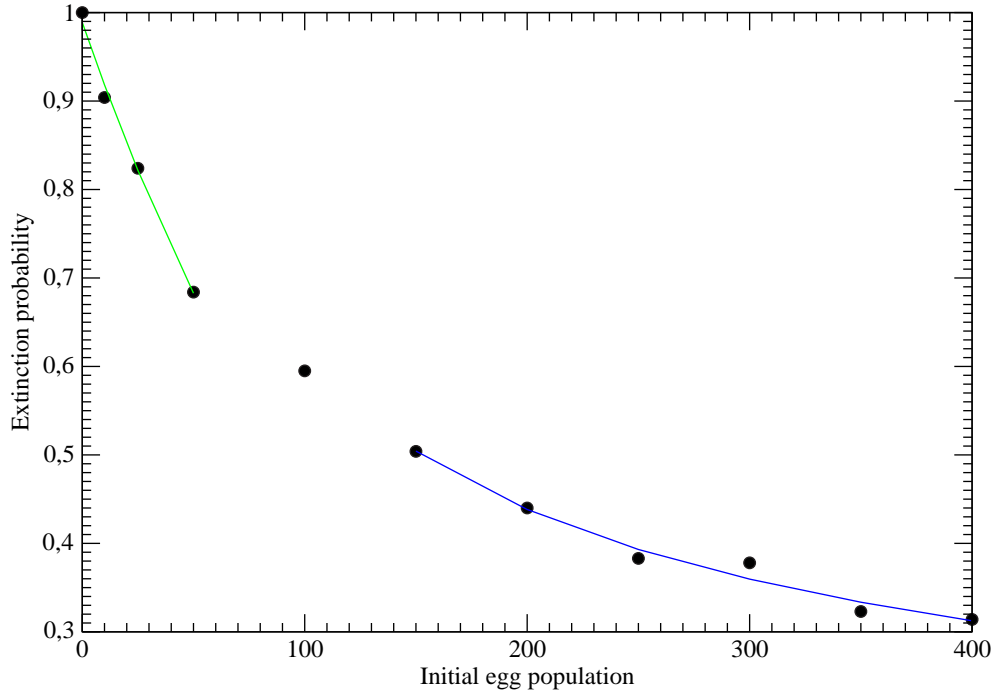
Fig. 11. The extinction probability after one year of evolution as a function of the initial condition. The population at the beginning of the runs was in the form of eggs. The probabilities of extinctions are computed as the number of runs that produced total extinction in 1000 runs. The number of breeding sites is $BS = 150$

the number of eggs follows from statistical independence ($P_{ext} = ((0.9926 \pm 0.03\%)^{eggs}$) are the fitted values).

However, for initial conditions larger than 100 eggs, the extinction probability follows a law of the form: $5.81(eggs)^{0.49 \pm 0.04}$ (the uncertainty corresponds to the standard deviation of the fitted coefficient). The point corresponding to 100 eggs is at border of the region with this dependence and far from the exponential dependence.

It is interesting to notice that the probability of extinction decreases more slowly when there are interactions than in the independent case. A result that can be attributed to the fact that the only interaction among individuals corresponds to an increase of mortality in the larval stage.

The number of eggs estimated on July 1st for $BS = 150$ and temperatures corresponding to Buenos Aires for an established population of mosquitoes is approximately 1000 according to our numeric simulations. Hence, nine of every ten eggs should be removed to achieve an extinction probability of 0.6. Furthermore, to achieve a probability of 0.8 less than 30eggs should remain, this is, half the average number of eggs laid by a female, requiring a very efficient eradication campaign.

8 Summary and conclusions

We have developed a stochastic model for *Aedes aegypti* populations based on the life cycle of the mosquito. The number of eggs, larvae, pupae, young female adults and female adults after the first oviposition are the five stages of the mosquito life included in the description.

The evolution of the subpopulations is considered in terms of ten random events with transition probabilities prescribed in terms of the biology of *Aedes aegypti* and the environment.

The model is able to deal with extinction processes and is ready for extensions to spatially heterogeneous environments and as such is particularly appropriated to study the potential evolution of *Aedes aegypti* populations in temperate climates.

The construction of the model has led us to a critical revision of the available data and modelling of the different biological events and several opportunities for improvements have been detected (see Section 5).

The model is based on realistic parameter values and we have shown that it is able to produce results that correspond well with field data not used as input for the model.

Based on our results we have discussed the temperature and environmental conditions that are needed for the survival of a local population of *Aedes aegypti*. Such data are critical for the design of eradication campaigns as well as for the evaluation of the effects of global weather changes in the distribution of the mosquito. The results indicate that average yearly temperature, seasonal temperature variation and numbers of breeding sites are relevant parameters required to evaluate the potential of a city to host a local population of *Aedes aegypti*.

The criterion introduced tentatively by Christophers resulting in a distribution limit based on the 10°C winter (July in the South, January in the North) isotherm was discussed concluding that the most relevant effect for temperate climates emerge from the number of breeding sites available for reproduction and the duration of the winter, rather than winter temperatures. The model fully supports an earlier criterion proposed by Carter [Carter (1931)] through the critical observation that *Aedes aegypti* can survive the winter in egg form.

The stochastic nature of the model allows for the maintenance of *Aedes aegypti* populations for a (random) number of years until extinction eventually occurs. A situation already envisioned by Carter as the likely case for the populations in Philadelphia and New York by the end of the eighteenth century. Such a

possibility contrasts with the conjecture that *Aedes aegypti* populations in ports were linked to summer infestations by mosquitoes landing from the boats that could not survive the first winter [Ministerio de Asistencia Social y Salud Publica (1964)].

The model also shows an important dependency of thresholds with the environment represented by the breeding site parameter. This feature explains the observations made during the eradication campaign in Argentina [Ministerio de Asistencia Social y Salud Publica (1964)] where the environment (where the mosquito thrived) changes from North to South following the general rule that the colder the site the higher the concentration of breeding sites required for finding *Aedes aegypti*.

While the stochastic model has a deterministic limit in terms of large population (as large as needed) we have shown numerically that such populations are several orders of magnitude larger than realistic homogeneous populations.

The criterion for the persistence of *Aedes aegypti* populations, discussed in this work, depends on the average yearly temperature, the seasonal variation and the carrying capacity of the environment. These data will change from city to city. Considering the maximum carrying capacity found at Buenos Aires cemeteries and the seasonal temperature amplitudes characteristic of Buenos Aires, the threshold for the persistence of the mosquito was roughly estimated to be the 15°C isotherm (average yearly temperature). This rough criterion is the result of a number of compromises with the data readily available. Temperature choices are then 10°C, 15°C and 20°C; carrying capacity represented by breeding sites and thermal amplitude corresponding to estimated values for Buenos Aires. Historical records of the presence of *Aedes aegypti* in Argentina below the 10°C July isotherm are consistent with this criterion, these latter records are also affected by uncertainties: were they just summer infestations or did the population persist, detected or undetected, at least one year? Infestations depend not only on favourable conditions but also on the probability of the mosquito reaching the city.

The introduced criterion helps to understand, and potentially explains, why *Aedes aegypti* has not been found in the Atlantic region below Buenos Aires (between approximately 38.5 °S to 38.0 °S on the Atlantic coast) in coincidence with a region with average yearly temperatures below 15°C but has been historically reported in Bahía Blanca (average yearly temperature 15.4°C) just south of this region on the Atlantic coast [2].

Finally, the fact that a large part of Buenos Aires city presents a density of

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[2] The climate in Bahía Blanca is greatly affected by the large amplitude of the ocean tides and the very shallow estuary that extends from Bahía Blanca to the north for a few hundred kilometres [Perillo and Piccolo (2004)].

breeding sites that cannot support populations of *Aedes aegypti* is in concordance with field results that suggest that repopulation processes are taking place every year during the warm season. The dynamics of such re-population processes in heterogeneous habitats requires the explicit inclusion of the space in the model as well as the biological and environmental data associated with the dispersal of mosquitoes.

Acknowledgements

A   Appendix: the Poisson approximation

We shall briefly describe in this appendix the main ideas involved in the Poisson approximation for a density-dependent Markov process.

Let X be an integer vector having as entries the populations under consideration, and $e_\alpha, \alpha = 1 \ldots \kappa$ the events at which the populations change by a fixed amount Δ_α in a Poisson process with density-dependent rates. Then, a theorem by Kurtz [Ethier and Kurtz (1986)] allows us to rewrite the stochastic process as:

$$X(t) = X(0) + \sum_{\alpha=1}^{\kappa} \Delta_\alpha Y(\int_0^t (\omega_\alpha(X(s))ds \tag{A.1}$$

where $\omega_\alpha(X(s)$ is the transition rate associated with the event α and $Y(x)$ is a random Poisson process of rate x.

This expression is the starting point for several approximations. In particular, the deterministic limit is obtained for transition rates of the form $\omega_\alpha(X) = N\Omega_\alpha(X/N)$ (a relation known as the mass-action law) and considering the stochastic variable X/N in the limit $N \to \infty$ for fixed t [Kurtz (1970)] (in this approximation only the mean values of the Poisson variables are relevant).

The deviations from the deterministic limit scaled by a factor $1/\sqrt{N}$ correspond in the same limit to a Brownian process [Kurtz (1971); Andersson

and Britton (2000)] (in this case, the Poisson variables are approximated by Gaussian variables).

The Poisson approximation to the stochastic process represented by equation (A.1) consists in introducing a self-consistent deterministic approximation for the arguments of the Poisson variables $Y(x)$ in equation (A.1) [Solari and Natiello (2003b); Aparicio and Solari (2001)]. The rationale under such a proposal is that the transition rates change at a slower rate than the populations. The number of each kind of event is then approximated as independent Poisson processes with deterministic arguments satisfying a differential equation.

The probability of n_α events of type α having occurred after a time dt is approximated by a Poisson distribution with parameter λ_α. Hence, the probability of the population taking the value

$$X = X_0 + \sum_{\alpha=1}^{\kappa} \Delta_\alpha n_\alpha \tag{A.2}$$

at a time interval dt after being in the state X_0 is approximated by a product of independent Poisson distributions of the form

$$\text{Probability}(n_1 \ldots n_\kappa, dt/X_0) = \prod_{\alpha=1}^{\kappa} P(\lambda_\alpha) \tag{A.3}$$

Finally,

$$d\lambda_\alpha/dt = <\omega_\alpha(X)> \tag{A.4}$$

where the averages are taken (self-consistently) with the proposed distribution ($\lambda_\alpha(0) = 0$). Actually, there are some small ($O(dt^2)$) corrections to this presentation when one of the populations is one event away from extinction [Solari and Natiello (2003b)]. Such correction has not been implemented in the present case because the extinction processes are very slow.

From the Poisson approximation it is possible to recover the deterministic equation and the Brownian approximation of the fluctuations in the proper limit. The approximation is accurate not only in the $N \to \infty$ (with fixed t) limit, but also in the infinitesimal time limit when the average number of events is small. It is this latter property what makes it specially suitable for the study of a process involving extinction.

The use of the Poisson approximation represents a substantial saving of computer time compared to direct (Monte Carlo) implementations of the stochastic process.

The details of the particular implementation for the population dynamics of the *Aedes aegypti* are tedious. The computer code, written in C, can be requested from the corresponding author.

B Stability analysis of the trivial solution

We refresh stability theory in this appendix, further details can be read in (Hill (1877); Wiggins (1988); Solari et al. (1996))

The deterministic model (1) presents coefficients that depend periodically on time through the temperature, equation (10). The phase space of the problem is then $(R^+)^5 S^1$ with R^+ the non-negative real numbers and S^1 the one dimensional circle corresponding to the time of the year. The trivial solution is then $(L, P, A1, A2, H, t) = (0, 0, 0, 0, 0, t)$.

Small perturbations of the trivial solution will evolve according to the linear equation (11). Notice that the fate of a perturbation, for example the introduction of a few adults, will not only depend on the type of the perturbation but also the time of the year in which it was produced, since it is not the same to introduce the adults under unfavourable winter conditions as during the favourable summer time. If the perturbation performed at t_0 is x_0 its time evolution is $x(t) = M(t, t_0)x_0$. The evolution up to a time $t + s$ consists in further integrating the problem by a time s with initial condition $x(t)$, hence $M(t+s, t_0) = M(t+s, t)M(t, t_0)$ which is nothing but the semi-group property for the flow.

The long time evolution of a perturbation of the trivial state, say after a time $t - t_0 = kyears + s$, with k integer, will be given by $M(t, t_0) = M(s + t_0, t_0)M(1year + t_0, t_0)^k$ where we have used that $M(t + nyear, nyear + t_0) = M(t, t_0)$ for n integer.

Hence, any perturbation will have the trivial solution as time-infinite limit if all of the eigenvalues of $M(1year + t_0, t_0)$ are smaller than one in absolute value (asymptotic stability). Further notice that the eigenvalues of $M(1year + t_0, t_0)$ are exactly the same than those for $M(1year, 0)$ since both matrices are conjugated by $M(t_0, 0)$

$$M(1year + t_0, t_0)M(t_0, 0) = M(t_0, 0)M(1year, 0) = M(1year + t_0, 0)$$

meaning that the stability does not depend of the time of the year chosen as t_0.

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