ORIGINAL ARTICLE

A Stochastic Spatial Dynamical Model for Aedes Aegypti

Marcelo Otero^{a,*}, Nicolás Schweigmann^b, Hernán G. Solari^a

^aDepartment of Physics, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

^bDepartment of Genetics and Ecology, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

Received: 13 September 2006 / Accepted: 19 December 2007 © Society for Mathematical Biology 2008

Abstract We develop a stochastic spatial model for *Aedes aegypti* populations based on the life cycle of the mosquito and its dispersal. Our validation corresponds to a monitoring study performed in Buenos Aires. Lacking information with regard to the number of breeding sites per block, the corresponding parameter (BS) was adjusted to the data. The model is able to produce numerical data in very good agreement with field results during most of the year, the exception being the fall season. Possible causes of the disagreement are discussed. We analyzed the mosquito dispersal as an advantageous strategy of persistence in the city and simulated the dispersal of females from a source to the surroundings along a 3-year period observing that several processes occur simultaneously: local extinctions, recolonization processes (resulting from flight and the oviposition performed by flyers), and colonization processes resulting from the persistence of eggs during the winter season. In view of this process, we suggest that eradication campaigns in temperate climates should be performed during the winter time for higher efficiency.

Keywords Mathematical ecology · Population dynamics · *Aedes aegypti* · Stochastic model · Dengue epidemics · Temperate climate · Spatial model · *Aedes aegypti* dispersal

1. Introduction

Dengue is an arboviral disease mainly transmitted by the mosquito *Aedes aegypti* and in the last years has become a major international public health concern (WHO, 1998, 2002). It is found in tropical and subtropical regions around the world, predominantly in urban and semiurban regions. As early as 1916, an epidemic of Dengue in Argentina affected the cities of Concordia and Paraná, and yellow fever epidemics decimated Buenos Aires between 1852 and 1905 (*Aedes aegypti* is also the main vector of yellow fever). In 1947, the Panamerican Health Organization led a continental mosquito eradication program, which was performed along the Americas and was based on the

^{*}Corresponding author.

E-mail address: mjotero@df.uba.ar (Marcelo Otero).

use of an insecticide (DDT) and the systematic destruction of breeding sites (BS) (Ministerio de Asistencia Social y Salud Publica, 1964). By 1967, the mosquito was considered to be eradicated in 18 countries including Argentina. But in 1986, it was detected in Posadas, Puerto Iguazú, and other cities in northern Argentina, and finally in Buenos Aires by 1995. Nowadays, the *Aedes aegypti* is a permanent inhabitant of Buenos Aires at least since its detection (Schweigmann and Boffi, 1998; de Garín et al., 2000; Carbajo et al., 2001). Dengue disease is not present in Buenos Aires and its surroundings, but it is present in tropical regions of Argentina, i.e., in the northern provinces of Salta, Jujuy, and Misiones (Funcei, 1998; Funcei 1999a, 1999b). Consequently, the possibility of epidemics in Buenos Aires cannot be ruled out.

Several interesting experimental and field studies were performed since the beginning of the twentieth century in order to study the dispersal of Aedes aegypti. These studies seem to show different and contradictory results because the experimental conditions during the experiments and observational studies influence dramatically the dispersal pattern of the mosquitoes. In contrast, only one spatial model for Aedes aegypti dispersal was developed until now. Takahashi et al. developed a simple deterministic model for Aedes aegypti dispersal that accounts for the effect of wind (Takahashi et al., 2005) and predicts the existence of stable traveling waves in several situations. However, in order to design a realistic dispersal model for *Aedes aegypti* in a city with temperate climate such as Buenos Aires, several factors have to be taken into account: the biology of the mosquito, the temperature seasonal variation, the spatial heterogeneity of the environment mainly represented by the availability of breeding sites (BS), and, of course, the dispersal of female adult mosquito populations, which is supposed to be driven by the availability of oviposition sites, since the female flies in order to deposit her eggs (Reiter et al., 1995; Edman et al., 1998; Muir and Kay, 1998). The abundance and dispersal of adult females are the key factors for the transmission of infectious diseases such as Dengue and yellow fever. For that reason, the dispersal pattern of adult females need to be studied and modeled.

In a previous paper (Otero et al., 2006), we have described a stochastic dynamical model for the evolution of *Aedes aegypti* in terms of a (nonlinear or state dependent) Markov chain (Ethier and Kurtz, 1986) considering four life stages of the mosquito: egg, larva, pupa, and adult. For every life stage, the relevant changes were modeled in terms of random events with temperature dependent rates determined from the biological data available for *Aedes aegypti*. These rates depend on time through the seasonal temperature changes. This previously published model is able to describe the seasonal changes of all mosquito populations in a homogeneous place where all mosquitoes have access to the oviposition sites, and because of this reason, the flight of adults was not considered in the model.

The aim of this work is to model the spatial population dynamics of *Aedes aegypti* in a temperate city like Buenos Aires and under natural conditions, understanding by natural conditions those in which the mosquitoes fly freely and naturally in search of breeding sites, and without the stress caused by capture-release experiments or by manipulations such as staining, marking or proboscis amputation.

In this article, we extend the previously developed model to an explicit spatial model, in which the space is represented by a collection of patches where an homogeneous dynamics takes place, complemented with interactions between patches. A mesh or grid of patches is considered and the interactions among them are fixed through population dispersal coefficients. Fixing the rules of the local dynamics and the interactions between patches (dispersal), extinction and repopulation processes occur naturally.

Studies performed in Buenos Aires (Carbajo et al. 2001, 2004) suggest that extinctions of all forms of the mosquito as well as repopulation processes are common in localized areas of the city. In fact, cemeteries and many neighborhoods are suitable places for the mosquito development and may act as sources. Hence, the city cannot be handled as an homogeneous place, and consequently, there is a need to incorporate the spatial heterogeneity and the female dispersal driven by the availability of breeding sites.

In what follows, we shall describe the basic biology of *Aedes aegypti* (Section 2), the *Aedes aegypti* dispersal (Section 3), the formulation of the spatial model (Section 4), the evaluation of parameters based on the biological data (Section 5), and the environmental and weather parameters of the model (Section 6).

In Section 7, we briefly indicate some factors not included in the model that could be relevant in other situations or for different mosquito species. Model results are presented in Section 8. The last section is dedicated to the summary, discussion, and conclusions.

2. Aedes aegypti: Adult and immature stages

The *Aedes aegypti* is a domestic mosquito that presents three immature stage types: egg, larva, and pupa.

Eggs are laid by adult females on wet surfaces, just above the water level. In their original environment, the breeding sites corresponded to tree-holes, however, exotic populations in urban habitats rely on small artificial containers such as cans, buckets, flower pots, and bottles placed in yards, gardens, and even inside houses. Eggs can resist low temperatures and they hatch when are mature and get wet, generating the larvae (Christophers, 1960).

Aedes aegypti larvae go through four stages (instars) in a period of a few days, depending on the temperature, and the last instar culminates in the pupal stage (pupation). The larval stage is the only immature form of the mosquito that eats and it is supposed that the natural regulation of *Aedes aegypti* populations occur due to intraspecific competition for food and other resources in this stage. While adults, which also eat, are capable of flying in search of food, larvae cannot and are restricted to live and eat in the container where they were born (Southwood et al., 1972; Dye, 1982; Subra and Mouchet, 1984; Gleiser et al., 2000).

The pupal stage lasts from one day to a few ones (depending on the temperature) at the end of which the adult emerges from the pupal skin (adult emergence) with a sex ratio of 1 to 1 (Southwood et al., 1972).

The adult stage of the mosquito is considered to last an average of 11 days in the urban environment (Horsfall, 1955; Christophers, 1960; Fay, 1964). Adult females are the ones which are involved in the propagation of infectious diseases. They lay an average of 63 eggs at each oviposition and this number changes according to its weight and several other factors (Arrivillaga and Barrera, 2004). The gonotrophic cycle is regulated by the temperature and is longer for the first oviposition than for the subsequent ones (Christophers, 1960). *Aedes aegypti* females bite humans in order to get a blood meal and complete their gonotrophic cycle and oviposit. However, they are also capable of biting other vertebrates

to get a blood meal in case of absence of humans (which is not the case in Buenos Aires, since the human density is more than enough to sustain the *Aedes aegypti* populations and, therefore, human availability is not a limiting factor).

3. Aedes aegypti dispersal

We open this section with a word of caution. The meaning and proper use of the words dispersal and migration applied to insects has been the subject of a long discussion in the biological field. The conclusion of the discussion was produced by Service following an invitation by the Entomological Society of America (Louisville meeting, Kentucky, 1996).

Appetential flights refer to dispersal or trivial flight, also termed creeping flights or movements by other entomologists that cease when certain goals are achieved, such as feeding, sheltering, and egg laying. Such flights are usually over short distances, such as a few hundred meters although longer flights of ≥ 1 km may be necessary if hosts and oviposition sites are widely separated. Appetential flights are referred to sometimes as active dispersal because they are self-propelled and self-steered— Nonappetential flights serve no special physiological need and are usually at the mercy of environmental factors such as wind and are characteristically unidirectional. Such flights are sometimes called passive dispersal. (Service, 1997)

We will consider all flights of Aedes aegypti as dispersal in accordance with Service.

The long distance dispersal of *Aedes aegypti* is performed by wind, ships, trucks, or public transport. In the nineteenth century, slave ships (The Baltimore clippers) introduced *Aedes aegypti* from West Africa into the Americas. The larvae were supposed to be present in the drinking water (Laird, 1989; Calder and Laird, 1994). Other ships transported *Aedes aegypti* to South Pacific, South Asia, and America, for example, the ship "Wellington" introduced *Aedes aegypti* in Hawaii in the nineteenth century.

We will not consider in the present work this long dispersal because in urban locations, transport by wind is not so likely as in open fields, and in any case, it applies to mosquitoes "whose flight takes them out of their boundary layer into the upper air," (Service, 1997) a situation not reported for *Aedes aegypti*. Other features such as urbanization are more relevant to this particular species. Nevertheless, it would be straightforward to modify the model to account for a drift in a predetermined direction.

3.1. Long distance flights

In 1909, the International Sanitary Convention of American Republics states in its quarantine regulations for yellow fever under article 45, paragraph 5: "The ship infected with yellow fever shall be moored at least 200 meters from an inhabited shore." This distance was in agreement with the results obtained later by Boyce in 1911, who estimated the range of flight of *Aedes aegypti* as 100 m and a maximum flight shorter than 200 m (Boyce, 1911). In 1927, Dunn showed in a field study performed in Nigeria that *Aedes aegypti* manifested a preference for oviposition in water containers located outside of houses, with bushes and trees nearby to provide places of rest and protection from the sun, as compared with containers of similar type inside houses (Dunn, 1927). The World Health Organization WHO, published in 1951, an international sanitary regulation in relationship with *Aedes aegypti* in which it is stated that all larvae and adults of *Aedes aegypti* had to be eliminated within a radius of 400 m from the airports.

Several experiments showed that *Aedes aegypti* is capable of flying long distances. Shannon and Davis released 12,000 mosquitoes stained with methylene blue from a sailing vessel anchored in one of the side arms of the bay in Bahia, Brazil. The vessel was 300 m from the eastern shore and 900 m from the western shore. Two days after the release, one mosquito was found in a house on the western shore at a distance of 950 m from the boat, and one day later, six more were found at distances of almost one kilometer. Four days after the release, 13 other mosquitoes were captured on the eastern shore at distances between 330 m and 1 km from the boat (Shannon et al., 1930). Wiseman et al. showed that Aedes aegypti is capable of crossing water up to 732 m (Wiseman et al., 1939). In 1949, Bugher and Taylor performed four releases of 266,000 radioactive Aedes aegypti mosquitoes in Nigeria and observed a maximum dispersal of 1165 m, which is supposed to have been influenced by wind, and it was observed that the more mosquitoes were released, the larger was the maximum distance traveled and the larger was the maximum life span registered for the mosquitoes (Bugher and Taylor, 1949). Wolfinsohn and Galun performed in 1953 two releases of gravid females in the center of a circular area of 5 km diameter in the desert of Israel. The two experiments (performed with different density of collecting-egg jars along the desert area) showed that only a small fraction of the released mosquitoes crossed over 2.5 km. The amount of eggs found at the border of the area is supposed to be influenced not only by wind, but also by jar density (Wolfinsohn and Galun, 1953). In 1995, Reiter et al. showed that rubidium marked ovipositing females are able to fly beyond 400 meters (Reiter et al., 1995). In 2003, Honorio et al. performed an experiment in Brazil that shows a maximum distance of at least 800 m in 6 days. In this experiment, the tip of the proboscises of all rubidium marked mosquitoes were cut off and the amount and location of available oviposition sites in the study area was changed. Consequently, it is possible that the mosquito manipulations and environmental changes influence the dispersal pattern of the released mosquitos and the experimental results (Honório et al., 2003).

All the experiments mentioned above emphasize the fact that the mosquito can reach long distances even if most of the released mosquitoes traveled shorter distances or were not captured or found. As a matter of fact in these experiments, the tails of the distributions are the center of attention and not the mean values.

Although long distance dispersal, like all extremes and records, attracts most attention and has curiosity value, short distance dispersal is undoubtedly the norm in mosquito biology. (Service, 1997)

3.2. Short distance flight

Although many experiments show long distance flights of *Aedes aegypti*, many others show in contrast a very short dispersal of the mosquito.

In an experiment performed by Morlan in Savannah, Georgia in 1958, females between 2 and 10 days of age were released within a city block. In 72 hours, 78% of the recovered mosquitoes flew a distance less than 22.86 m, 18% a distance between 22.86 m, and 53.34 m, 4% a distance between 53.34 m and 83.82 m (Morlan and Hayes, 1958). In another release, in an experiment performed by McDonald (in Kenya, 1977), most adult Aedes aegypti dispersed less than 20 meters and the majority of those recaptured were collected in the same house where they were released (McDonald, 1977). Trpis and Häusermann calculated a mean daily flight for females of 57 meters, with a maximum dispersal of 154 meters. 60% of the mosquitoes released were found in houses within 50 meters from their release point (Trpis and Häusermann, 1986). Rodhain and Rosen stated in 1997 that spontaneous dispersal of adults averages from 30 to 50 m per day, so that females are rarely expected to visit more than 2 or 3 houses in their lifetime (Rodhain and Rosen, 1997). In 1998, Muir et al. measured a mean distance traveled of 56 m for females and 35 m for males. The maximal distance traveled was 160 m and the daily dispersal was between 16.8 m and 24.7 m for females and between 14.7 m and 18.2 m for males (Muir and Kay, 1998). In Iquitos, Peru, a spatial analysis agrees with the preponderant evidence that most adults do not fly far from the container where they developed as larvae and pupae (Getis et al., 2003). Ordoñez-Gonzalez et al. calculated a maximum dispersal distance of 120 m and a mean dispersal distance of 30.5 m (Ordoñez-Gonzalez et al., 2001). Harrington et al. showed in a release-recapture experiment that the majority of released mosquitoes were collected at their release or the adjacent house. Only a few flew a maximum distance of 512 m (Harrington et al., 2005).

3.3. Dispersal driven by the availability of oviposition sites

One of the main questions about *Aedes aegypti* dispersal is the motivation of the flight. We have already said that the female adult must bite and take a blood meal to complete the oogenesis and to deposit the eggs in the breeding sites. Ovaries of female Aedes aegypti undergo a maturation period (gonotrophic cycle) of approximately 2-5 days (temperature dependent) and during which the female does not blood feed. Dispersal and long flights in search of food during this time would increase the female's chance of being damaged or killed by predators without increased reproductive success; therefore, it would be advantageous for females to remain near release sites or breeding sites until ready to blood feed and oviposit. Afterwards, the dispersal is increased, and this increase may be associated with the search for oviposition sites (Muir and Kay, 1998). Once the females are able to deposit their eggs, they fly in order to find oviposition sites. If the density of oviposition sites is high, females find them rapidly and the resulting dispersal is short. Instead, if the density of breeding sites is low, they have to fly long distances until they find one suitable place to oviposit. Some experimental results and observational studies indicate that the Aedes aegypti dispersal is driven by the availability of oviposition sites (Wolfinsohn and Galun, 1953; Reiter et al., 1995; Edman et al., 1998). Actually, the experimental results of flights in the desert by Wolfinsohn and Galun (1953) might also illustrate this effect rather than the inhibition of flight by wind suggested by the authors.

3.4. Factors affecting the dispersal pattern

Several factors seem to affect the dispersal pattern of *Aedes aegypti*: availability of cool, dark, resting places (Dunn, 1927), availability of vegetation and nectar sources, location, amount and availability of oviposition sites and mates (Reiter et al., 1995; Edman et al., 1998; Muir and Kay, 1998), wind direction (Wolfinsohn and Galun, 1953; Bugher and

Taylor, 1949), rainfall, housing characteristics (McDonald, 1977), blood sources (Human or other vertebrates), etc.

All the previously mentioned studies were performed in different experimental and field conditions. Consequently, the results of the dispersal studies are supposed to be affected by the factors described above and also by the physical characteristics of the study site (urban or village), the distribution pattern of houses around release sites (Tsuda et al., 2001), urbanization: presence of houses, buildings, yards, streets, avenues, parks, etc. (Carbajo et al., 2006). Also, weather conditions of the study locations such as temperature, humidity, wind, and rainfall are very influential; it is worth noticing that all studies were performed in very different environments: urban, wild, desert, etc. The physiological state of the mosquitoes on the release day: age, blood feed, stage in the gonotrophic cycle, and the stress produced during the manipulation of the mosquitos before and during the release (staining, marking, proboscis amputation) seem to be a determining influence in the studies.

In this article, we will distinguish three kind of females: adult females in their first gonotrophic cycle (A1 females), females in subsequent gonotrophic cycles (A2 females), and flyers (F), which are the adult females who have already finished their gonotrophic cycles and fly in order to deposit their eggs. The availability of food, mates, and humans was not incorporated into the model because these variables are not limiting factors in a temperate city such as Buenos Aires.

4. Mathematical model

We consider the two dimensional space as a mesh or grid of rectangular patches where the local dynamics takes place, and we let the adult mosquitoes (flyers) fly from patch to patch. The coordinates of a patch are given by two indexes, *i* and *j*, corresponding to the row and column in the grid. If X_1 is a population stage in mosquito life cycle, then $X_1(i, j)$ is the X_1 population of this stage in the patch of coordinates (i, j).

The model considers six different populations: eggs $E_{(i,j)}$, larvae $L_{(i,j)}$, pupae $P_{(i,j)}$, female adults not having laid eggs $A1_{(i,j)}$, flyers $F_{(i,j)}$, and female adults having laid eggs $A2_{(i,j)}$. The population of adult male mosquitoes is not taken into account explicitly and we consider that one half of the emerging adults are females (Southwood et al., 1972). We also consider that during the gonotrophic cycles the mosquito dispersal is negligible, and once the gonotrophic cycle ends, the female begins to fly, becoming a Flyer $F_{(i,j)}$ in search of oviposition sites.

4.1. Local events

The evolution of the six populations in each patch is affected by twelve different possible local events: death of eggs, egg hatching, death of larvae, pupation, death of pupae, adult emergence, completion of gonotrophic cycles, death of young adults $A1_{(i,j)}$, oviposition by $F_{(i,j)}$ flyers, death of $A2_{(i,j)}$ adults, and death of $F_{(i,j)}$. 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. Table 1 summarizes this information.

Table 1 Event type, effects on the populations and transition rates for the developmental model. The coefficients are cycle1, cycle2: gonotrophic cycle coefficient (number of daily cycles) for adult females in stages A1 and A2.; $\operatorname{ovr}_{(i,j)}$: oviposition rate by flyers in the (i, j) patch; egn: average number of eggs laid in an oviposition; me: mortality of eggs; elr: hatching rate; ml: mortality of larvae; α : 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. The values of the developmental and mortality rates are available in Appendix A

Event	Effect	Transition rate
1° Gonotrophic cycle (1)	$A1_{(i,i)} \rightarrow A1_{(i,i)} - 1$	
	$F_{(i,i)} \rightarrow F_{(i,i)} + 1$	$w_1 = \text{cycle1} * A_{1(i,i)}$
2° Gonotrophic cycle (2)	$A2_{(i,i)} \rightarrow A2_{(i,i)} - 1$	
	$F_{(i,j)} \rightarrow F_{(i,j)} + 1$	$w_2 = \text{cycle2} * A2_{(i, j)}$
Oviposition (3)	$E_{(i,j)} \rightarrow E_{(i,j)} + \text{egn}$	
	$F_{(i,j)} \rightarrow F_{(i,j)} - 1$	
	$A2_{(i,j)} \rightarrow A2_{(i,j)} + 1$	$w_3 = \operatorname{ovr}_{(i,j)} * F_{(i,j)}$
Egg death (4)	$E_{(i,j)} \rightarrow E_{(i,j)} - 1$	$w_4 = \operatorname{me} * E_{(i,j)}$
Egg hatching (5)	$E_{(i,j)} \rightarrow E_{(i,j)} - 1$	
	$L_{(i,j)} \to L_{(i,j)} + 1$	$w_5 = \operatorname{elr} * E_{(i,j)}$
Larval death (6)	$L_{(i,j)} \rightarrow L_{(i,j)} - 1$	$w_6 = ml * L_{(i,j)} + \alpha * L_{(i,j)} * (L_{(i,j)} - 1)$
Pupation (7)	$L_{(i,j)} \to L_{(i,j)} - 1$	
	$P_{(i,j)} \to P_{(i,j)} + 1$	$w_7 = \operatorname{lpr} * L_{(i,j)}$
Pupal death (8)	$P_{(i,j)} \to P_{(i,j)} - 1$	$w_8 = (mp + par * (1 - (ef/2))) * P_{(i,j)}$
Adult emergence (9)	$P_{(i,j)} \rightarrow P_{(i,j)} - 1$	
	$A1_{(i,j)} \to A1_{(i,j)} + 1$	$w_9 = \text{par} * (\text{ef}/2) * P_{(i,j)}$
$(A1_{(i,j)})$ Death (10)	$A1_{(i,j)} \to A1_{(i,j)} - 1$	$w_{10} = \operatorname{ma} * A1_{(i,j)}$
$(A2_{(i,j)})$ Death (11)	$A2_{(i,j)} \to A2_{(i,j)} - 1$	$w_{11} = \max * A2_{(i,j)}$
Flyer Death (12)	$F_{(i,j)} \to F_{(i,j)} - 1$	$w_{12} = \operatorname{ma} * F_{(i,j)}$

4.2. Flyers dispersal

The general rate of the dispersal event is given by:

$$w = \beta * F_{(i,j)} \tag{1}$$

with

$$\beta = \begin{cases} 0 & \text{if the patches are disjoint,} \\ \text{diff}/d_{ij}^2 & \text{if the patches have at least a common point,} \end{cases}$$
(2)

where d_{ij} is the distance between the centers of the patches and diff is a diffusion-like coefficient. For a typical patch not in the border of the habitat, adults can directly fly to eight different patches, with the patches at the corners having a dispersal rate compatible with a diffusion-like process.

We suppose that the area of a patch is about 1 ha (a normal city block in Buenos Aires) and we discriminate two types of flights:

Perpendicular flights when a $F_{(i,j)}$ can fly to four possible patches with indexes: (i + 1, j), (i - 1, j), (i, j + 1) and (i, j - 1), with a rate:

$$w_{(13)} = \beta_p * F_{(i,j)},\tag{3}$$

where β_p is the dispersal coefficient for perpendicular flights.

And diagonal flights when a $F_{(i,j)}$ can fly to four possible patches with indexes: (i + 1, j + 1), (i - 1, j - 1), (i - 1, j + 1) and (i + 1, j - 1), with a rate:

$$w_{(14)} = \beta_d * F_{(i,j)},\tag{4}$$

where β_d is the dispersal coefficient for diagonal flights.

For a patch of 1 ha, $d_{ij} = 100$ m for the perpendicular flight and $d_{ij} = 100 * \sqrt{2}$ m for the diagonal flight, then $\beta_d = \beta_p/2$.

We assumed two different diffusion-like coefficients for the simulations: diff = $830 \text{ m}^2/\text{day}$ which corresponds to a short dispersal, approximately a mean dispersal of 30 m in one day and diff = $8,300 \text{ m}^2/\text{day}$ corresponding to a mean dispersal of approximately 90 m in one day. These chosen diffusion-like coefficients are in agreement with the short dispersal experiments and field studies analyzed in Section 3, which were performed under the most natural conditions. We compared the simulation results obtained with these two different diffusion-like coefficients in Section 8.

Boundary conditions of two types have been considered. In the first boundary condition, the probability of flying away from the region under study was considered equal to the probability of flying into that region. A zero average derivative condition that assumes that the patch is just part of a larger region with the same favorable conditions for the mosquitoes. The second type of boundary condition used in the model is a no-come-back condition in which mosquitoes fly away from the region under study but do not fly into it, i.e., implying a zero population of flying females outside the region considered. While the second type of condition implies an effective higher mortality for the whole population, the effect is not important, representing a correction to the estimated number of breeding sites from BS \approx 15–25 into BS \approx 20–30 (see Section 8).

4.3. Stochastic dynamic model

The evolution of the populations is modeled by a (state dependent) Poisson process (Ethier and Kurtz, 1986; Andersson and Britton, 2000) where the probability of the state:

$$(E_{(i,j)}, L_{(i,j)}, P_{(i,j)}, A1_{(i,j)}, A2_{(i,j)}, F_{(i,j)})$$

evolves in time following a Kolmogorov forward equation that can be constructed directly from the information collected in Table 1 and subsection Flyers dispersal. Figure 1 shows the populations and events of the *Aedes aegypti* life cycle stochastic model.

The numerical implementation of the stochastic model was performed with fixed time steps of 10^{-4} day using a Poisson approximation (Solari and Natiello, 2003).

Density dependent stochastic models have associated deterministic differential equation models (Kurtz, 1970, 1971, Ethier and Kurtz, 1986) which are useful in the limit of infinite size population with finite population density, but are not appropriate in situations of low populations such as extinction situations. As reference, the associated deterministic model is presented in Appendix B.



Fig. 1 Populations and events of the stochastic model, where $w_{(k)}$ with k = 1, 2, ..., 14 are the transition rates of Table 1 and Section 4.2.

5. Biological parameters

The rates of occurrence of the events described in Table 1 are specified for the case of *Aedes aegypti*. Consequently, the different parameters appearing in the stochastic process described by Table 1 characterize *Aedes aegypti* biology.

5.1. Developmental and mortality rates

The five developmental rates that correspond to egg hatching, pupation, adult emergence, and gonotrophic cycles are evaluated using the results of the thermodynamic model developed by Sharpe and DeMichele (1977) and were described in detail in the previous article (Otero et al., 2006). The different mortality rates as well as the emergence rate have been taken from Focks et al. (1993), Christophers (1960) and were also described previously (Otero et al., 2006). The values of the developmental and mortality rates are available in Appendix A.

5.2. Breeding site dependent oviposition rate

Outside laboratory conditions, not every water container would be a breeding site. The efficiency of the process of egg laying in the appropriate places (breeding sites) will be less than one. It just may happen that in a given homogeneous patch, there are no breeding sites and the eggs laid in the patch will not develop up to the adult stage.

When considering as patches areas larger than the natural roaming area of the mosquito and a low amount of breeding sites, the efficiency of the females in locating an ecologically place for egg laying, i.e., a breeding site, has to be incorporated into the model. We introduce thus a multiplicative factor

$$0 < \theta \le 1 \tag{5}$$

affecting oviposition rates to account for the difficulties of locating isolated breeding sites, clearly when there are no breeding sites available (BS = 0) the modeled female continues her search for an oviposition site (the ability of *Aedes aegypti* of postponing oviposition has been documented Chadee, 1997).

According to Christophers (1960), the average time for egg deposition is tdep = 0.229 days in laboratory conditions. Having no extra information, we choose $\theta = (BS_{(i,j)})/150$ as a linear function of the breeding sites.

In the described oviposition rate, we suppose that if there are at least 150 BS in a patch, then the mosquito could find a breeding in an average time given by tdep. Hence, if the number of breeding sites is equal or greater than 150, the oviposition coefficient is the reciprocal of the oviposition time in laboratory conditions, tdep. If the amount of breeding sites is lower than 150, then the oviposition coefficient is lower and proportional to the amount of breeding sites. The threshold 150 BS is a bit arbitrary, and corresponds to approximately one breeding site in an area of 67 m², i.e., an area of approximately $8 \text{ m} \times 8 \text{ m}$. We suppose that if there is only one BS in an area of $8 \text{ m} \times 8 \text{ m}$, a mosquito is able to find it. Simulations performed with other values of this threshold, e.g., 300 BS, present no significant differences in the observed results.

The oviposition rate is then

$$w_3 = \operatorname{ovr}_{(i,j)} * F_{(i,j)} \tag{6}$$

with

$$\operatorname{ovr}_{(i,j)} = \begin{cases} \theta / \operatorname{tdep} & \text{if } BS_{(i,j)} \le 150, \\ 1 / \operatorname{tdep} & \text{if } BS_{(i,j)} > 150. \end{cases}$$
(7)

As we can see in (6), only female flyers $F_{(i,j)}$ deposit eggs and once they have deposited the eggs they become adults $A2_{(i,j)}$. Then egg deposition and the change from flyer $F_{(i,j)}$ to adult $A2_{(i,j)}$ are the same event. Accordingly, the oviposition rate depends on the amount of breeding sites; the dispersal time depends also on the amount of breeding sites, and then mosquito dispersal is driven by the availability of oviposition (breeding) sites.

5.3. Nonlinear larval mortality rate

In Section 2, we have said that the natural regulation of *Aedes aegypti* populations occurs due to intraspecific competition for food and other resources in the larval stage. This mechanism reflects not only a characteristic of the species but also a characteristic of the environment.

The simplest way to introduce this mechanism is through a nonlinear correction to the larval mortality, i.e.,

$$\omega_6(L_{(i,j)}) = mlL_{(i,j)} + \alpha L_{(i,j)} * (L_{(i,j)} - 1)$$
(8)

the value of α can be further decomposed as

$$\alpha = \alpha_0 / \text{BS}_{(i,j)} \tag{9}$$

with α_0 being associated with the carrying capacity of one breeding site and BS_(*i*,*j*) being the amount of breeding sites in the (*i*, *j*) patch. The value of α_0 was fitted to observed values in the cemeteries of Buenos Aires (Otero et al., 2006).

In this model, we have not considered the possible effect of inhibition of egg eclosion due to the increase of the larval density (Livdahl et al., 1984) because it was not observed in field studies.

6. Environmental and weather parameters

The discussion of the mosquito life under constant temperature makes sense only for laboratory studies, but in a real environment (urban or village), the mosquito will be exposed to seasonal temperature changes. In what follows, we have adopted two different strategies:

- (a) The use of real data: the measured mean daily temperatures for the period July 2001–July 2002. Since no local climate data of Mataderos quarter were available, the daily mean temperatures considered in the model were those of Buenos Aires, which were taken from the Aeroparque Station of the Servicio Meteorológico Nacional of Argentina, approximately 10 km from Mataderos quarter (Data available at US Department of Commerce). Taking into account the proximity of the Aeroparque Station to Mataderos quarter, the similar environment, and the approximations and the level of detail made in our model, we consider that the available weather data used in the simulations are adequate.
- (b) The use of a simple model for mean daily temperature variation that contains only the deterministic component of the temperatures. The model was chosen from Király and Jánosi (2002) and takes the form:

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

with the time measured in days beginning on the first of July. The parameters a, b, and c were fitted from temperature records along a period of time of 10 years and are: $a = 18.0 \,^{\circ}\text{C}$; $b = 6.7 \,^{\circ}\text{C}$, and c = 9.2. The use and development of this model is detailed in Otero et al. (2006).

We make the assumption that the mean daily temperature of breeding sites is equal to the mean daily temperature of the air, and we define a breeding site as a water container without high exposure to the sun and in places without predators. Consequently, not every water container is a potential breeding site.

7. Some factors not included in the model

There are a number of factors that influence the development of *Aedes aegypti* and have not been incorporated into the model so far. These factors may be relevant for other cli-

mates and environmental situations than those in our target. We list the main factors not included:

Dependence of mortality with humidity. Relevant in regions with dry seasons.

Rainfalls. Relevant if breeding sites depend on them for water and they are not regularly distributed such as in dry-humid climatic alternations. The contribution of watering by humans usually plays a compensating role.

Tree and shrub cover. *Aedes aegypti* needs nectar for its nutrition, as well as resting places sheltered from the sun.

Urbanization. Not only the availability of breeding sites is not uniform in a city, but also different kinds of constructions can disturb the flying of mosquitoes. For example, walls not taller than 5 m were found to separate different population densities in Buenos Aires cemeteries (Vezzani et al., 2004). Wide avenues may become obstacles for dispersal across them while displacement along street directions might be favored.

It can be speculated that winds may also play a role and introduce a bias in the dispersal so that a net convective effect emerges on average. This possibility cannot be ruled out but it should be noticed that it goes against the urbanization factor. Actually, if 5 m tall walls imply an obstacle for the dispersal of the mosquito, then they are very unlikely to fly high enough so that prevalent winds drags them. Passive dispersal by wind is not considered in general among the most relevant mechanisms for urban mosquitoes (Service, 1997).

Seeking blood meals. It can be argued that *Aedes aegypti* may be forced to disperse in search of blood meals. Not relevant unless a high spatial resolution is being considered, a resolution being able to distinguish between the houses and the proximities of peoples' houses where *Aedes aegypti* lives. The range of this appetential flight is characteristically short for *Aedes aegypti*.

Low human populations. At least in speculative terms, one could consider the fate of *Aedes aegypti* mosquitoes born at breeding sites with such low densities of human beings in the area (as well as substitute vertebrates) that the blood meals become a limiting factor. However, this situation seems farfetched.

8. Results

8.1. Monitoring study in a quarter of Buenos Aires: Mataderos

From 1998 to 2001, a study directed at *Aedes aegypti* surveillance was performed in Buenos Aires, the study consisted in the search for *Aedes aegypti* eggs in ovitraps distributed in 280 sites in Buenos Aires. During this study, it was found that the city of Buenos Aires is not a homogeneous place, in relation to the development of *Aedes aegypti*. The distribution of the mosquito depends on the vegetation, the human population density, and the demographic and urban characteristics of the different quarters (Carbajo et al., 2001, 2004, 2006). During this study in Buenos Aires, it was observed that the Mataderos quarter was a place within the city, in which the proportion of positive ovitraps presented some of the highest rates of the city during the summer months. Consequently, between July 2001 and July 2002, an *Aedes aegypti* monitoring study was performed in part of the Mataderos quarter. The field study consisted in a planned weekly monitoring



Fig. 2 Rainfalls (a), temperature (b) and fraction of positive ovitraps with confidence bands (c) along the period of monitoring between the first week of July 2001 and the last week of June 2002.

study of approximately 120 ovitraps distributed in a rectangular region of 12×5 blocks of the quarter.

Figure 2 shows the rainfall distribution (a), the daily mean temperature (b) and the fraction of positive ovitraps (with the 90% confidence bands) (c) along one year, from July 2001 up to July 2002 (data available at US Department of Commerce, 2006). As we can see in Fig. 2, the rainfall distribution was homogeneous during the year and there is no evidence of influence of the seasonal rainfalls in the proportions of positive ovitraps. On the contrary, as it was shown in the previous work (Otero et al., 2006) a delay between the maximum of the populations and the maximum of temperature is observed. The 90% confidence bands for the proportion of positive ovitraps were calculated; for details, see Appendix C.

8.2. Sampling model

Let a city block or patch contain BS breeding sites, and suppose that all breeding sites are equivalent, so a female that oviposits her eggs will do it in a particular breeding site with a probability of $p = \frac{1}{BS}$. Then we put two ovitraps in every patch in order to sample the number of eggs, p becomes $p = \frac{1}{(BS+2)}$. The ovitraps are supposed to have the same breeding quality as the natural breeding sites and are supposed to be distributed homogeneously among the natural breeding sites. The correction to the egg mortality due to the removal of eggs was not considered.



Fig. 3 Fraction of positive ovitraps in Mataderos with confidence bands and q calculated with the spatial model with flight for different amount of BS and different diffusion-like coefficients (a) = $830 \text{ m}^2/\text{day}$ and (b) = $8300 \text{ m}^2/\text{day}$.

Let us calculate the probability q that given M ovipositions during a week; there was at least one oviposition $(k \ge 1)$ in the ovitraps. Since this process is binomial with a success probability p, we have

$$P(k/M) = \binom{M}{k} * p^{k} * (1-p)^{M-k},$$
(11)

$$q = P([k \ge 1]/M) = 1 - {\binom{M}{0}} * p^0 * (1-p)^{M-0}$$
(12)

with $p = \frac{1}{(BS+2)}$.

Now, having a sampling model, we will use the developed spatial model to calculate the weekly ovipositions M.

8.3. Estimation of the breeding site density

Figure 3 shows the fraction of positive ovitraps in Mataderos along one year, between July 2001 and July 2002, and the values of q calculated with the stochastic spatial model with flight for different amount of BS. We performed the simulations using a grid with 12×5 patches (corresponding to the 60 blocks of the quarter), all patches with the same amount of breeding sites (BS) and with two different diffusion-like coefficients (a) diff = $830 \text{ m}^2/\text{day}$ and (b) diff = $8300 \text{ m}^2/\text{day}$. The temperature used in the simulations were



Fig. 4 Probability for the next year extinction as a function of the density of breeding sites (BS) for an isolated patch without flight and with the seasonal temperature of Buenos Aires. The inset shows the probabilities vs. BS in semilogarithmic scale.

the real daily mean temperatures between July 2000 and July 2002. We started with 10,000 eggs in every patch the first of July 2000 and we ran the simulation for 2 years. Then we calculated the number of weekly ovipositions in the second year of the simulation (July 2001–July 2002) and estimated the value of q. This procedure was repeated for different amounts of breeding sites (between 10 and 500 BS) and we compared the field results with those obtained in the simulations. Only the simulation results for 15, 20, and 25 BS are shown in Fig. 3.

From the simulations that roughly fit the experimental data, we could estimate the density of BS in Mataderos as 15–25 BS. We also observed that the density of breeding sites is almost independent of the value of the diffusion-like coefficient at least in the range $830-8300 \text{ m}^2/\text{day}$.

Although we observed a very good match between the field data and the simulation results for 15–25 BS during winter, spring, and summer, there is no good fit at the beginning of fall when the fraction of positive ovitraps falls faster in the field than in the simulations. Several simulations were performed changing the border conditions and values of different parameters of the model such as: diffusion-like coefficients, BS threshold of the oviposition rate, fecundity of the females, etc., but no observable improvement of the fits was detected. Other factors not included in the model such as the increase of the population of mosquito predators at the end of summer and beginning of fall might be the causes of the fast fall of the fraction of positive ovitraps.

8.4. Flight as a persistence strategy

Isolated patches with the seasonal temperature of Buenos Aires and less than 15–25 breeding sites have a next year survival probability less than 0.5 (Otero et al., 2006). Figure 4



Fig. 5 Positivity of ovitraps simulated with and without dispersal for 20 breeding sites per patch, 12×5 blocks, initial conditions of 10,000 eggs per block. Without dispersal, the population gets extinct by the third year, with dispersal (diff = 830 m²/day) it reaches a recurrent state. The points indicate measured values.

shows the probability of extinction of all mosquito populations in the second year for an isolated patch without dispersal ($\beta = 0$) as a function of the breeding site density. The probabilities were estimated as the proportion of extinctions in 300 simulations.

In Fig. 5, we compare the ovitrap positivity along 10 years simulated with and without dispersal for 20 BS/patch in a grid of 12×5 patches (blocks) with an initial condition of 10,000 eggs per block. As we can see without dispersal, the population gets extinct by the third year, as was expected since the next year survival probability for this breeding site density is less than 0.5, but with dispersal (diff = $830 \text{ m}^2/\text{day}$) it reaches a recurrent state. The points in Fig. 5 indicate the measured values. The temperature used in the simulations corresponds to (10).

As a matter of fact, the mosquito dispersal seems to be an advantageous strategy for the mosquito to survive in a hostile/marginal environment where the density of breeding sites is low and the climate conditions are marginal for the mosquito development. Consequently, the persistence of *Aedes aegypti* in a temperate city such as Buenos Aires requires dispersal mechanisms.

Figure 6 shows the field data of Mataderos quarter and the simulation results performed with the spatial model such as was already done in Section 8.3, but in this case without flight and for 150 BS, an amount of breeding sites for which the next year extinction probability is equal or less than 0.01. As we can see in Fig. 6, the probability (q)reaches one during summer and there is no match between field and simulation results. It is also important to notice that (yearly recurrent) dispersal in the marginal environment



Fig. 6 Value of q calculated with the spatial model without flight for 150 BS/patch and experimental data with its confidence bands.

discussed above is evidenced by populations that do not reach the carrying capacity of the environment (compare Figs. 6 and 3).

Field data of Buenos Aires city indicate that *Aedes aegypti* is not detected in some quarters until January, an observation that suggested that recurrent dispersal-extinction cycles were present (Schweigmann et al., 2002).

8.5. Two dimensional dispersal simulations

As we have already said, during the monitoring study between 1998 and 2001, it was found that the city of Buenos Aires is not a homogeneous place in relation to the development of *Aedes aegypti*. The Mataderos quarter seems to be an ideal place for the development of the mosquito and we could imagine that this quarter may act as source of mosquitoes for the surrounding areas.

We simulated the dispersal of the mosquitoes from one border of the quarter (with a density of 20 BS/patch) to the adjacent quarter with a decreasing gradient of BS, decreasing 1 BS per patch (block). Then our simulation grid correspond to a rectangle grid of 21×12 patches (21 rows and 12 columns). We run the simulation along three hypothetical years beginning the first of July. The initial conditions were: 10,000 eggs/patch in the source border (12 patches of the first row) and no eggs in the other 240 patches. The diffusion-like coefficient chosen was 830 m²/day and the temperature was calculated using the deterministic model, (10). We analyzed two different but complementary results of the simulation: the spatial distribution of eggs and the spatial distribution of the oviposition activity.

In Fig. 7, we can see the evolution of the spatial distribution of the *Aedes aegypti* accumulated alive eggs along the grid in the third year of the simulation. The bottom



(a) July 1^{st}



(b) August 1^{st}



(c) September 1^{st}



(d) October 1^{st}



(e) November 1^{st}



(f) December 1^{st}



(g) January 1^{st}



(h) February 1^{st}



(i) March 1^{st}



(j) April 1^{st}





(l) June 1^{st}

Fig. 7 Spatial distribution of eggs.

row corresponds to the first row or border of the source with 20 BS/patch and the top row (row 21) has a density of BS of 0.1 BS/patch. Completely black squares correspond to patches without eggs, and completely white squares correspond to patches with the maximum amount of eggs during the summer. The gray scale indicates amounts of eggs between zero and the maximum in a logarithmic scale.

If we analyze the pictures corresponding to the months of July to October (end of winter and beginning of spring), we can see the local extinction of the eggs in the grid. However, eggs remain at several patches in the bottom half of the grid. In spring and beginning of the summer, the amount of eggs increases rapidly as a result of the eclosion of the remaining eggs and repopulation processes performed by flyers coming from the bottom rows. Since January, we can see an expansive wave from the zone with higher amount of breeding sites to the zone with lower amount of breeding sites reaching almost the top row. The last picture, corresponding to June, shows again the beginning of the local extinctions.

Meanwhile in Fig. 8, we can see the evolution of the weekly oviposition activity, along the grid in the third year of the simulation. Only the first week of every month is shown. Completely black squares correspond to patches without oviposition activity, and completely white squares correspond to patches with the maximum oviposition activity during the summer. In this case, the gray scale indicates oviposition activity between zero and the maximum in a logarithmic scale.

As we can see, there is almost no oviposition activity during the winter and beginning of spring, except of a few random ovipositions, which is in agreement with the fact that in Figs. 7(a) to (d) only local extinctions of eggs are observed. By the end of spring begins the oviposition activity in the bottom half of the grid corresponding to the zone with higher density of breeding sites. During the summer, a wave front is observed from the zone with high density to the zone of low density of breeding sites. In fall, the oviposition activity gradually begin to fall and finally no activity is observed during the winter.

In conclusion, because of the existence of remaining eggs in the surroundings the dispersal process from the source is not only a simple recolonization process from zones with high density of BS to zones with lower density of BS, instead several processes occur simultaneously along the year such as local extinctions, recolonization processes as a result of the flight, and oviposition of flyers and reemergence of adults as a result of the eclosion of remaining eggs.

Figure 9 shows the dependence of the mean and deviation of eggs during winter and summer with the density of breeding sites in the simulation described above. Since the death of eggs is the most relevant event of the cold season, it is relevant to explore how the differences between summer and winter in the number of eggs can be attributed to this factor. As the death of eggs is an individual process, we expect a roughly exponential decay with time. This is to say that the population of eggs in winter and summer can be related by a expression of the form:

$$\operatorname{Eggs}(\operatorname{BS}, t_w)/\operatorname{Eggs}(\operatorname{BS}, t_s) = \operatorname{Exp}(\gamma(t_s - t_w))$$
(13)

with γ (close to) the egg mortality rate, t_w and t_s the time in winter and summer, respectively.

As we can see in Fig. 9 for fixed times, $t_w = 1$ (1st of July) and $t_s = 210$ (1st of February), the mean of eggs is roughly linear in the range 7–20 BS. Under the hypothesis



Fig. 8 Weekly oviposition activity.

leading to (13), Eggs(BS, t_w)/Eggs(BS, t_s) would be constant with the density of breeding sites. The inset in Fig. 9 shows the dependence of the ratio Eggs(BS, 1)/Eggs(BS, 210) with BS. This dependence is almost constant with BS in the zone of high density of BS



Fig. 9 Mean and Standard Deviation of Eggs in summer and winter as a function of the density of breeding sites. The inset shows the dependence of the ratio between Eggs in winter and summer with the density of breeding sites.

but a negative slope is observed corresponding to a slight growth of the ratio in the zone of low density of BS. We attribute the increase in the low BS density zone to the repopulation of these regions. The population of adult mosquitoes increases continuously all summer up to the fall, the eggs remaining in the winter in the unfavorable regions are (mostly) laid at the end of the adult flying season. This use of marginal regions increases the chances for eggs to survive the winter.

9. Summary and conclusions

We have developed the first stochastic spatial model for *Aedes aegypti* populations based on the life cycle of the mosquito and its dispersal. The populations of eggs, larvae, pupae, young female adults, flyers, and female adults after the first oviposition are the six stages of the mosquito life included in the description. The evolution of the populations is considered in terms of fourteen random events with transition probabilities prescribed in terms of the biology of *Aedes aegypti* and the local environment.

The model uses realistic parameter estimations and only one of them is an "adjustable" parameter that accounts for the availability of breeding sites in the environment, BS. There are three parameters that have been taken with some degree of arbitrariness, the average number of eggs laid in an oviposition which biologically depends on the weight of the females (Arrivillaga and Barrera, 2004), the dispersal coefficient for which we only have rough estimations, and the ability of the mosquito to locate breeding sites, represented by the parameter θ in (7), an aspect of the mosquito life that has not received attention

by biologists in the past. The model has shown high sensitivity only to the number of breeding sites.

The model is able to deal with the mosquito dispersal and can be used to estimate the amount of effective breeding sites of a homogeneous place from the fraction of positive ovitraps in that region, obtained as a result of a surveillance study without altering the environment and without perturbation of the mosquito populations. For example, we estimated the density of breeding sites of a Buenos Aires quarter Mataderos as 15–25 BS/ha.

The construction of the model has led us to a critical review of the literature about experiments and field studies performed to estimate the mosquito dispersal and to an analysis of its different and (seemingly) contradictory results, concluding that the experimental conditions influence dramatically the obtained results.

The results of the simulations for the Mataderos quarter, when compared with the field data collected, indicate that the model reproduces the observed positivity in the ovitraps during spring and summer, but over estimates the fraction of positive ovitraps in fall. Our working hypothesis is that there are some biological relevant (dynamical) processes that need to be incorporated into the model, such as, for example, season dependent predatory pressure. It is worth noticing that even when only the total number of ovipositions are considered, there are visible and measurable effects of the dispersal-extinction process. This result contrasts with a well-educated guess that spatially-homogeneous models are able to show the skeleton of the biological problem (Durrett, 1999). In the present case, the number of breeding sites apparently present in Buenos Aires would warrant the extinction of *Aedes aegypti* in a spatially homogeneous model and more than twice the number of breeding sites estimated would be necessary at least at some place (reservoir) for the mosquito to survive.

Simulations of the dispersal of females from a zone with high density of breeding sites to a zone with low density of breeding sites along three years allowed us to observe that because of an incomplete extinction of eggs during the winter in the zones of low density of BS, the dispersal process from the source is not only a simply recolonization process from zones with high to low density of breeding sites. Instead, several processes occur simultaneously along the year such as local extinctions, recolonization processes as a result of the flight and oviposition of flyers, and reemergence processes as result of the eclosion of remaining eggs. This observation would be in agreement with the fact that a large part of Buenos Aires presents a density of breeding sites that cannot support populations of *Aedes aegypti* and that Buenos Aires is at the border of the present day geographical distribution of *Aedes aegypti* in South America.

Although risk free dispersal out of a fully exploited environment can be easily argued to be an advantageous strategy for the mosquito, the situation simulated does not fall into this simple category. The mosquitoes do not reach the carrying capacity of the environment as can be seen by the absence of a summer-plateau in the field data (and then in the simulated situation). Actually, the simulations support the idea that the survival of *Aedes aegypti* in Buenos Aires is not related to the presence of reservoirs, but actually relies on a stochastically recurrent dispersal-extinction cycle. Eggs survive the winter season at random patches and from these patches the recovering of the population begins each spring.

The model indirectly imposes costs to the dispersal strategy, since the search of breeding sites, particularly when they are scarce, takes time and the mosquito may lose the Poisson race between oviposition and death. For the populations of mosquitoes in a marginal environment such as Buenos Aires, the dispersal strategy makes the difference between extinction in a short number of years or persistence. Since urban settings with temperate climate are not the original environment of *Aedes aegypti*, one has to wonder how this evolutionary trait was acquired.

We conclude that for a large city in a temperate climate, focusing exclusively on potential reservoirs (such as cemeteries) might not be an efficient strategy to carry out the eradication of the mosquito since the mosquito can survive in distributed environments, locally below the breeding site density needed for survival in isolation. The dispersal strategy of *Aedes aegypti* in search of breeding sites also suggests that winter eradication campaigns, consisting in potential breeding sites removal, would be more efficient that summer campaigns. In winter, only immature stages are present, which cannot disperse, while in summer, adults could fly away to find an available place to oviposit driven by the removal of potential breeding sites.

Acknowledgements

The authors acknowledge CONICET and the support given by the University of Buenos Aires under grant X308 and by the Agencia Nacional de Promoción Científica y Tecnológica (Argentina) under grant PICTR 87/2002.

Appendix A: Developmental and mortality rates

A.1 Developmental rates

There are five developmental rates in the model that correspond to egg hatching, pupation, adult emergence, and the first and following gonotrophic cycles. These rates are evaluated using the results of the thermodynamic model developed by Sharpe and DeMichele (1977) and simplified by Schoofield et al. (1981).

According to this model for poikilothermal development, the maturation process is controlled by one enzyme which is active in a given temperature range and is deactivated only at high 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

$$R_D(T) = R_D(298\,^\circ\text{K}) \frac{(T/298\,^\circ\text{K}) * \exp((\Delta H_A/R)(1/298\,^\circ\text{K} - 1/T))}{1 + \exp(\Delta H_H/R)(1/T_{1/2} - 1/T))}, \qquad (A.1)$$

where ΔH_A and ΔH_H are thermodynamics enthalpies characteristic of the organism, R is the universal gas constant, and $T_{1/2}$ is the temperature when half of the enzyme is deactivated because of high temperature.

In Table A.1, we present the values of the different coefficients involved for the events: egg hatching, pupation, adult emergence, and gonotrophic cycles. The values are taken from Focks et al. (1993) and are discussed in Otero et al. (2006).

A.2 Mortality, fecundity and emergence rates

The different mortality rates as well as the emergence rate have been taken from Focks et al. (1993), Christophers (1960) and are as follows:

Develop. cycle (A.1)	$R_D(T)$	$R_D(298^{\circ}\mathrm{K})$	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)	cycle1	0.216	15725	1756481	447.2
Gonotrophic c. (A2)	cycle2	0.372	15725	1756481	447.2

Table A.1 Coefficients for the enzymatic model of maturation (A.1). R_D is measured in day⁻¹, enthalpies are measured in (cal/mol) and the temperature is measured in absolute (Kelvin) degrees

Egg mortality The mortality of the eggs is chosen to be me = 0.011/day and is independent of the temperature in the range $278 \text{ }^\circ\text{K} \le T \le 303 \text{ }^\circ\text{K}$ (Trpis, 1972).

Larva mortality The death of the larvae is divided in two contributions as explained previously. One contribution accounts for natural mortality under optimal conditions and depends only on the temperature. Its rate is approximated by $ml = 0.01 + 0.9725 \exp(-(T - 278)/2.7035)$ and is valid in the range $278 \text{ }^{\circ}\text{K} \leq T \leq 303 \text{ }^{\circ}\text{K}$ (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 and was already described in Section 5.3.

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

Adult mortality The mortality of adults is considered independent of temperature. The mortality rate for an adult is ma = 0.091/day in the range $278 \degree K \le T \le 303 \degree K$ (Horsfall, 1955; Christophers, 1960; Fay, 1964).

Fecundity 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 3-day-old female is 1.35 mg (Christophers, 1960), hence we estimate the average number of eggs laid in one oviposition as egn = 63.

Emergence Besides the daily mortality in the pupal stage, there is an additional mortality associated with the emergence of the adults. We consider 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 ef = 0.83 and multiplies the developmental rate of the pupa already described (Southwood et al., 1972).

Appendix B: Deterministic model

The deterministic model associated to the stochastic model reads:

$$\frac{dE_{(i,j)}}{dt} = \operatorname{egn} * \operatorname{ovr} * F_{(i,j)} - \operatorname{me} * E_{(i,j)} - \operatorname{elr} * E_{(i,j)},$$
(B.1)

$$\frac{dL_{(i,j)}}{dt} = \operatorname{elr} * E_{(i,j)} - \operatorname{ml} * L_{(i,j)} - \alpha * (L_{(i,j)})^2 - \operatorname{lpr} * L_{(i,j)},$$
(B.2)

$$\frac{dP_{(i,j)}}{dt} = \operatorname{lpr} * L_{(i,j)} - \operatorname{mp} * P_{(i,j)} - \operatorname{ef} * \operatorname{par} * P_{(i,j)} - (1 - \operatorname{ef}) * \operatorname{par} * P_{(i,j)}, (B.3)$$

$$\frac{dA1_{(i,j)}}{dt} = \text{par} * (\text{ef}/2) * P_{(i,j)} - \text{ma} * A1_{(i,j)} - \text{cycle1} * A1_{(i,j)}, \tag{B.4}$$

$$\frac{dF_{(i,j)}}{dt} = \text{cycle1} * A1_{(i,j)} + \text{cycle2} * A2_{(i,j)}$$

- ovr * $F_{(i,j)}$ - ma * $F_{(i,j)} - 4 * \beta_d * F_{(i,j)} - 4 * \beta_p * F_{(i,j)}$
+ $\beta_p * (F_{(i,j+1)} + F_{(i,j-1)} + F_{(i+1,j)} + F_{(i-1,j)})$
+ $\beta_d * (F_{(i+1,j+1)} + F_{(i-1,j-1)} + F_{(i+1,j-1)} + F_{(i-1,j+1)}),$ (B.5)

$$\frac{dA2_{(i,j)}}{dt} = \text{ovr} * F_{(i,j)} - \text{cycle2} * A2_{(i,j)} - \text{ma} * A2_{(i,j)}.$$
(B.6)

Appendix C: Confidence intervals

We present our estimation of approximate confidence interval for a binomial proportion, despite being a classical material in statistics books, we find that the most frequent presentations are not useful close to extinctions.

Consider *N* independent Bernoulli trials with constant success probability *p*, and let *n* be the number of successes in a random sample of size *N*. A success is observed if X_i , with i = 1, 2, ..., N, has a specific characteristic and a failure is observed if X_i does not have that characteristic. The proportion of successes in the sample is denoted as q = n/N, and *p* indicates the theoretical frequency.

Then

$$P(|p-q| \le z_{(1-\alpha)/2} * \sigma(p, N)) \simeq (1-\alpha)$$
(C.1)

with $\sigma(p, N) = \sqrt{p(1-p)/N}$ and where z is the $z_{(1-\alpha)/2}$ quantile of the standard normal distribution.

For the extremes of the interval, the equality $|p - q| = z_{(1-\alpha)/2} * \sigma(p, N)$ is true then:

$$|p-q| = z_{(1-\alpha)/2} \sqrt{p(1-p)/N},$$
(C.2)

$$(p-q)^{2} = (z_{(1-\alpha)/2})^{2} p(1-p)/N.$$
(C.3)

Solving this second grade equation, we obtain the two extremes of the confidence interval. Notice that when q = 0, the confidence interval is $[0, 1 - 1/z_{(1-\alpha)/2}]$.

References

Andersson, H., Britton, T., 2000. Stochastic Epidemic Models and Their Statistical Analysis. Lecture Notes in Statistics, vol. 151. Springer, Berlin.

- Arrivillaga, J., Barrera, R., 2004. Food as a limiting factor for *aedes aegypti* in water-storage containers. J. Vector Ecol. 29, 11–20.
- Bar-Zeev, M., 1957. The effect of density on the larvae of a mosquito and its influence on fecundity. Bull. Res. Council Israel B 6, 220–228.
- Bar-Zeev, M., 1958. The effect of temperature on the growth rate and survival of the immature stages of aedes aegypti. Bull. Entomol. Res. 49, 157–163.
- Boyce, R., 1911. Yellow Fever and Its Prevention. E.P. Dutton and Co., New York.
- Bugher, J.C., Taylor, M., 1949. Radiophosphorus and radiostrontium in mosquitoes. Preliminary report. Science 110, 146–147.
- Calder, L., Laird, M., 1994. Mosquito travellers, arbovirus vectors and the used tyre trade. Travel. Med. Int. 12, 3–12.
- Carbajo, A.E., Schweigmann, N., Curto, S.I., de Garín, A., Bejarán, R., 2001. Dengue transmission risk maps of Argentina. Trop. Med. Int. Health 6(3), 170–183.
- Carbajo, A.E., Gomez, S.M., Curto, S.I., Schweigmann, N., 2004. Variación espacio temporal del riesgo de transmisión de dengue en la ciudad de Buenos Aires. Medicina 64, 231–234.
- Carbajo, A.E., Curto, S.I., Schweigmann, N., 2006. Spatial distribution pattern of oviposition in the mosquito aedes aegypti in relation to urbanization in Buenos Aires: southern fringe bionomics of an introduced vector. Med. Vet. Entomol. 20, 209–218.
- Chadee, D.D., 1997. Effects of forced egg-retention on the oviposition patterns of female *aedes aegypti* (diptera:culicidae). Bull. Entomol. Res. 87, 649–651.
- Christophers, R., 1960. Aedes aegypti (L.), the Yellow Fever Mosquito. Cambridge Univ. Press, Cambridge.
- de Garín, A.B., Bejarán, R.A., Carbajo, A.E., de Casas, S.C., Schweigmann, N.J., 2000. Atmospheric control of aedes aegypti populations in Buenos Aires (Argentina) and its variability. Int. J. Biometerol. 44, 148–156.
- Dunn, L.H., 1927. Observations on the oviposition of *aedes aegypti* linn., in relation to distance from habitations. Bull. Ent. Res. 18, 145–148.
- Durrett, R., 1999. Stochastic spatial models. SIAM Rev. 41(4), 677-718.
- Dye, C., 1982. Intraspecific competition amongst larval *aedes aegypti*: Food exploitation or chemical interference. Ecol. Entomol. 7, 39–46.
- Edman, J.D., Scott, T.W., Costero, A., Morrison, A.C., Harrington, L.C., Clark, G.G., 1998. Aedes aegypti (diptera culicidae) movement influenced by availability of oviposition sites. J. Med. Entomol. 35(4), 578–583.
- Ethier, S.N., Kurtz, T.G., 1986. Markov Processes. Wiley, New York.
- Fay, R.W., 1964. The biology and bionomics of *aedes aegypti* in the laboratory. Mosq. News. 24, 300–308.
- Focks, D.A., Haile, D.C., Daniels, E., Moun, G.A., 1993. Dynamics life table model for aedes aegypti: Analysis of the literature and model development. J. Med. Entomol. 30, 1003–1018.
- FUNCEI, 1998. Dengue enfermedad emergente. Fund. Estud. Infectol. 1(1), 1-6, http://www.funcei.org.ar.
- FUNCEI, 1999a. Dengue enfermedad emergente. Fund. Estud. Infectol. 2(1), 1–12, http://www.funcei.org.ar.
- FUNCEI, 1999b. Dengue enfermedad emergente. Fund. Estud. Infectol. 2(2), 1-8, http://www.funcei.org.ar.
- Getis, A., Morrison, A.C., Gray, K., Scott, T.W., 2003. Characteristics of the spatial pattern of the dengue vector, *aedes aegypti*, in Iquitos, Peru. Am. J. Trop. Med. Hyg. 69(5), 494–505.
- Gleiser, R.M., Urrutia, J., Gorla, D.E., 2000. Effects of crowding on populations of aedes albifasciatus larvae under laboratory conditions. Entomol. Exp. Appl. 95, 135–140.
- Harrington, L.C., Scott, T.W., Lerdthusnee, K., Coleman, R.C., Costero, A., Clark, G.G., Jones, J.J., Kitthawee, S., Kittayapong, P., Sithiprasasna, R., Edman, J.D., 2005. Dispersal of the dengue vector *aedes aegypti* within and between rural communities. Am. J. Trop. Med. Hyg. 72(2), 209–220.
- Honório, N.A., da Costa Silva, W., Leite, P.J., Gonçalvez, J.M., Lounibos, L.P., de Oliveira, R.L., 2003. Dispersal of *aedes aegipty* and *aedes albopictus* (dipetera culicidae) in an urban endemic dengue area in the state of Rio de Janeiro, Brazil. Mem. Inst. Oswaldo Cruz 98, 191–198.
- Horsfall, W.R., 1955. Mosquitoes: Their Bionomics and Relation to Disease. Ronald, New York.
- Király, A., Jánosi, I.M., 2002. Stochastic modelling of daily temperature fluctuations. Phys. Rev. E 65, 051102.
- Kurtz, T.G., 1970. Solutions of ordinary differential equations as limits of pure jump Markov processes. J. Appl. Probab. 7, 49–58.

- Kurtz, T.G., 1971. Limit theorems for sequences of jump processes approximating ordinary differential equations. J. Appl. Probab. 8, 344–356.
- Laird, M., 1989. Vector-borne diseases introduced into new areas due to human movement: a historical perspective. In: Service, M.W. (Ed.), Demography and Vector-Borne Diseases, pp. 17–33. CRC, Boca Raton
- Livdahl, T.P., Koenekoop, R.K., Futterweit, S.G., 1984. The complex hatching response of *aedes* eggs to larval density. Ecol. Entomol. 9, 437–442.
- McDonald, P.T., 1977. Population characteristics of domestic aedes aegypti (diptera: Culicidae) in villages on the Kenya coast. ii. dispersal within and between villages. J. Med. Entomol. 14(1), 49–53.
- Ministerio de Asistencia Social y Salud Publica, A., 1964. Campaña de erradicacion del Aedes aegypti en la República Argentina. Informe final. Buenos Aires.
- Morlan, H.B., Hayes, R.O., 1958. Urban dispersal and activity of aedes aegypti. Mosq. News 18, 137-144.
- Muir, L.E., Kay, B.H., 1998. Aedes aegypti survival and dispersal estimated by mark-release-recapture in northern Australia. Am. J. Trop. Med. Hyg. 58, 277–282.
- Nayar, J.K., Sauerman, D.M., 1975. The effects of nutrition on survival and fecundity in Florida mosquitoes. Part 3. utilization of blood and sugar for fecundity. J. Med. Entomol. 12, 220–225.
- Ordoñez-Gonzalez, J.G., Mercado-Hernandez, R., Flores-Suarez, A.E., Fernandez-Salas, I., 2001. The use of sticky ovitraps to estimate dispersal of aedes aegypti in northeastern Mexico. J. Am. Mosq. Control Assoc., Inc. 17(2), 93–97.
- Otero, M., Solari, H., Schweigmann, N., 2006. A stochastic population dynamic model for *aedes aegypti*: formulation and application to a city with temperate climate. Bull. Math. Biol. 68, 1945–1974.
- Reiter, P., Amador, M.A., Anderson, R.A., Clark, G.G., 1995. Short report: dispersal of aedes aegypti in an urban area after blood feeding as demonstrated by rubidium-marked eggs. Am. J. Trop. Med. Hyg. 52, 177–179.
- Rodhain, F., Rosen, L., 1997. Mosquito vectors and dengue virus-vector relationships. In: Gubler, D.J., Kuno, G. (Eds.), Dengue and Dengue Hemorragic Fever, pp. 61–88. CAB International, New York.
- Rueda, L.M., Patel, K.J., Axtell, R.C., Stinner, R.E., 1990. Temperature-dependent development and survival rates of culex quinquefasciatus and aedes aegypti (diptera: Culicidae). J. Med. Entomol. 27, 892–898.
- Schoofield, R.M., Sharpe, P.J.H., Magnuson, C.E., 1981. Non-linear regression of biological temperaturedependent rate models based on absolute reaction-rate theory. J. Theor. Biol. 88, 719–731.
- Schweigmann, N., Boffi, R., 1998. Aedes aegypti y aedes albopictus: Situación entomológica en la región. In: Temas de Zoonosis y Enfermedades Emergentes, Segundo Cong. Argent. de Zoonosis y Primer Cong. Argent. y Lationoamer. de Enf. Emerg. y Asociación Argentina de Zoonosis, pp. 259–263, Buenos Aires.
- Schweigmann, N., Orellano, P., Kuruc, J., Vera, M.T., Vezzani, D., Méndez, A., 2002. Distribución y abundancia de aedes aegypti (diptera: Culicidae) en la ciudad de Buenos Aires. In: Salomón, D.S. (Ed.), Actualizaciones en Artropodología Sanitaria Argentina, pp. 155–160.
- Service, M.W., 1997. Mosquito (diptera: Culicidae) dispersal-the long and short of it. J. Med. Entomol. 34, 579–588.
- Shannon, R.C., Burke, A.W., Davis, N.C., 1930. Observations on released stegomyia aegypti (1.) with special reference to dispersion. Am. J. Trop. Med. 10, 145–150.
- Sharpe, P.J.H., DeMichele, D.W., 1977. Reaction kinetics of poikilotherm development. J. Theor. Biol. 64, 649–670.
- Solari, H.G., Natiello, M.A., 2003. Stochastic population dynamics: the Poisson approximation. Phys. Rev. E 67, 031918.
- Southwood, T.R.E., Murdie, G., Yasuno, M., Tonn, R.J., Reader, P.M., 1972. Studies on the life budget of aedes aegypti in Wat Samphaya Bangkok Thailand. Bull. W.H.O. 46, 211–226.
- Subra, R., Mouchet, J., 1984. The regulation of preimaginal populations of *aedes aegypti* (l.) (diptera: Culicidae) on the Kenya coast. ii. food as a main regulatory factor. Ann. Trop. Med. Parasitol. 78, 63–70.
- Takahashi, L.T., Maidana, N.A., Ferreira, W.C. Jr., Pulino, P., Yang, H.M., 2005. Mathematical models for the aedes aegypti dispersal dynamics: Travelling waves by wing and wind. Bull. Math. Biol. 67, 509–528.
- Trpis, M., 1972. Dry season survival of aedes aegypti eggs in various breeding sites in the Dar es Salaam area, Tanzania. Bull. W.H.O. 47, 433–437.
- Trpis, M., Häusermann, W., 1986. Dispersal and other population parameters of aedes aegypti in an African village and their possible significance in epidemiology of vector-borne-diseases. Am. J. Trop. Med. Hyg. 35, 1263–1279.

- Tsuda, Y., Takagi, M., Wang, S., Wang, Z., Tang, L., 2001. Movement of *aedes aegypti* (diptera: Culicidae) released in a small isolated village on Hainan island, China. J. Med. Entomol. 38(1), 93–98.
- US Department of Commerce, 2006. National climatic data center, http://www.ncdc.noaa.gov/oa/ncdc. html.
- Vezzani, C., Velázquez, S.T., Schweigmann, N., 2004. Seasonal pattern of abundance of aedes aegypti (diptera: Culicidae) in Buenos Aires city, Argentina. Mem. Inst. Oswaldo Cruz 99, 351–356.
- WHO, 1998. Dengue hemorrhagic fever. Diagnosis, treatment, prevention and control. World Health Organization, Ginebra, Suiza.
- WHO, 2002. Dengue and Dengue hemorrhagic fever. World Health Organization, Ginebra, Suiza.
- Wiseman, R.H., Symes, L.B., McMahon, J.C., Teesdale, C., 1939. Report on a malaria survey of Mombasa. Nairobi Government Printer, Nairobi.
- Wolfinsohn, M., Galun, R., 1953. A method for determining the flight range of aedes aegypti (linn.). Bull. Res. Council Israel 2, 433–436.