



Brazilian Journal of Physics

ISSN: 0103-9733

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Sociedade Brasileira de Física

Brasil

Paixão, C. A.; C. Charret, I. C.; Lima, R. R.
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Brazilian Journal of Physics, vol. 42, núm. 1-2, 2012, pp. 132-136
Sociedade Brasileira de Física
São Paulo, Brasil

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Intraspecific Competition and Population Dynamics of *Aedes aegypti*

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Received: 12 July 2011 / Published online: 29 December 2011
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Abstract We report computational simulations for the evolution of the population of the dengue vector, *Aedes aegypti* mosquitoes. The results suggest that controlling the mosquito population, on the basis of intraspecific competition at the larval stage, can be an efficient mechanism for controlling the spread of the epidemic. The results also show the presence of a kind of genetic evolution in vector population, which results mainly in increasing the average lifespan of individuals in adulthood.

Keywords Dengue · Disease control · *Aedes aegypti* · Population dynamics · Genetic evolution

1 Introduction

Dengue is one of the major public health problems worldwide. The WHO estimated that about 2.5 billion people [1]—two fifths of world population—are now at risk. The WHO estimates that there may be 50 million dengue infections worldwide every year. The disease is now endemic in over 100 countries in Africa, Americas, Eastern Mediterranean, Southeast Asia, and Western Pacific. Southeast Asia and Western Pacific are the most affected areas. Before 1970, only nine countries

had outbreaks of dengue, a number that had increased more than fourfold by 1995.

Another source of concern is the explosive outbreaks of the disease. The tally in Venezuela reached 80,000 cases in 2007. In Brazil, according to the WHO, 21 deaths and 108,640 cases were recorded in January and February 2010. Such high numbers were attributed to the high precipitation and temperatures in the summer months and to the recirculation of serotype DEN-1 after 15 years. An epidemiological report from the Ministry of Health based on data collected until the 17th week in 2010 listed 737,756 reported cases and 321 deaths, a 94% increase in deaths in comparison with the same period in 2009.

In the absence of effective vaccines, one of the most common methods to curb dengue epidemics is the control of the vector mosquito *Aedes aegypti*. Effective control calls for good knowledge of the dynamics of population growth throughout the life cycle of the mosquito. Currently, the relative importance of certain features is known. For example, the intraspecific competition in the larval stage is an important factor, as well as the mosquitoes' ability to adapt to adverse environmental conditions [2, 3]. The intraspecific competition opposes members of the same species, individuals competing for food, water, light, and space. To develop effective control strategies, one must understand the effects of this mechanism, which limits the population, and of other factors upon the dynamics of infestation.

We present the computational study of a model describing the dynamics of vector-population growth. The model includes intraspecific competition and the possibility of genetic evolution. We pay special attention to the effect of the larval intraspecific competition

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upon the expansion of the adult population. We also study the influence of genetic evolution, under various environmental conditions. Genetic evolution being related to sexual reproduction, our model allows genetic recombination during the reproductive process.

The paper is organized as follows: In Section 2, we present the model and its parameters used. Results and discussion are presented in Section 3, and Section 4 collects our conclusions.

2 The Simulation Model

We follow previous analyses of population dynamics [4] and adopt a bitstring computational model. The main phenotypic characteristics of individuals are added to the model through these bitstrings. The simulation takes into account all the steps in the population development. This technique serves well the purposes of our research because it keeps track of hereditary transmission.

All the characteristics of an individual are added to the model through these bitstrings. Each individual receives a bitstring. During the reproductive process, a bitstring of a male and a female is randomly combined to generate the bitstrings of their descendants. The combination yields individuals with new genotypes, mimicking the evolution of the population.

The parameters in the simulation model were obtained from several papers reporting the characteristics of the species under study [5, 6]. They are associated with life development stages of the vector. For each stage, the values are generated according to the distributions reported in Table 1. The development stages of *A. aegypti* are egg, larva, pupa, and winged. In our treatment, the sex of each individual and the maximum number of eggs that each female can lay are generated

randomly. Each individual is able to move with a fixed step size, which is also generated randomly.

The total number of individuals in the simulation was kept at 10,000 U distributed on a square lattice with dimensions $8,192 \times 8,192$ length units. The carrying capacity for each development phase of the vector was taken to be 2,500 individuals. Oviposition occurred at fixed points of the square lattice, at the following positions: 100,100, -100,100, 100,100, and -100,100. The rate of intraspecific competition ranges from 0.0 (representing 0%) to 1.0 (100%) in steps of 0.2 (20%) in each simulation. The statistical distributions that generate the parameters controlling the vector features are described in Table 1.

3 Results and Discussion

Figure 1 presents the results for the temporal evolution of populations of egg, larva, pupa, and winged, with a competitive rate of 0.5 in all phases. Initially, 2,500 eggs were distributed randomly among the breeding. The population of eggs starts with 2,500 eggs and decays with time, as the eggs hatch and the larval population grows. Over time, the larval population reaches its carrying capacity and decreases. This decrease is due to transition to the pupal stage. Soon after, the mosquitoes begin to emerge. Note that after a few hours, the mosquitoes begin to breed and lay eggs. This is reflected in the growth of egg population. The laying and development of eggs boosts the other populations, and the process repeats. After 4,000 h, the populations stabilize.

Figure 2 presents the temporal evolution of the larval population for different rates of intraspecific competition. When the competition increases, the number of individuals is reduced. For values above 0.2, the

Table 1 Statistical distribution associated with model parameters

Model parameters	Statistical distribution	Distribution parameters
Development time of egg	Poisson	$\lambda = 3$ (36 h)
Development time of larvae	Poisson	$\lambda = 8$ (96 h)
Development time of pupae	Poisson	$\lambda = 6$ (72 h)
Lifetime of winged	Poisson	Male $\lambda = 10$ (120 h) Female $\lambda = 44$ (528 h)
Sex	Uniform	Lower limit = 0.0 Upper limit = 1.0
Step size of the displacement	Uniform	
Male mosquito		Lower limit = -50.0 Upper limit = 50.0
Female mosquito		Lower limit = -100.0 Upper limit = 100.0
Numbers of eggs	Poisson	$\lambda = 100$

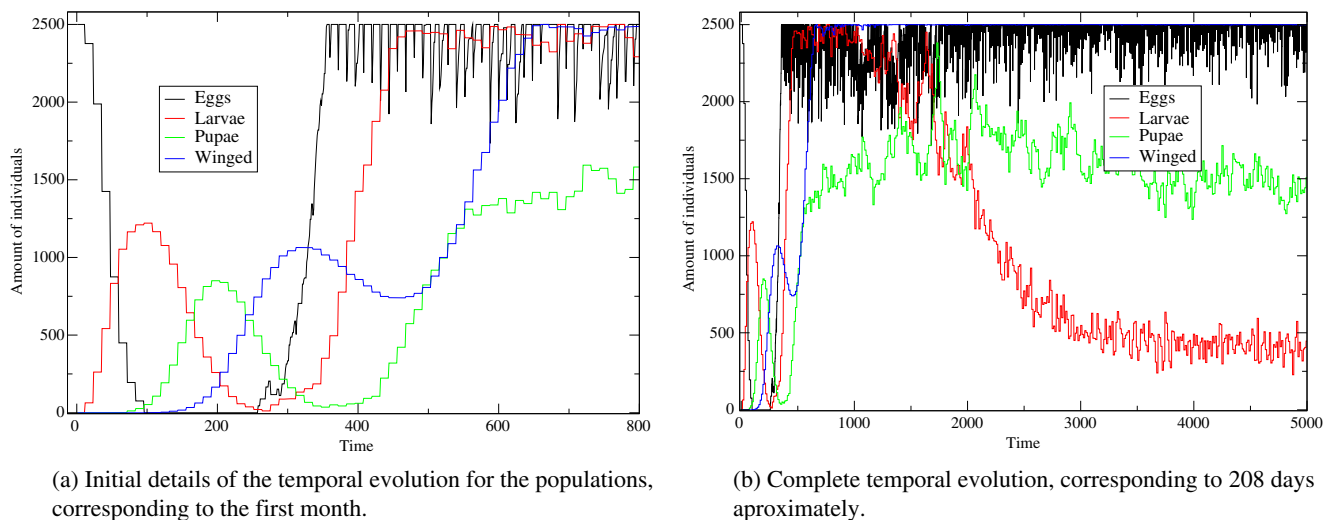


Fig. 1 Temporal evolution of populations of eggs, larvae, pupae, and mosquitoes, with intraspecific competition equal to 0.5 (50%) in each phase

number of larvae drops sharply. When the competition is unitary, the larvae are extinguished, and the extinction is carried over to the other phases of the population.

Figure 3 displays the evolution of the mosquito population for different rates of competition. For values above 0.6, the number of individuals is substantially smaller. The inset presents the evolution for rates of intraspecific competition between 0.8 and 0.9. Sufficiently high rates in this interval, roughly above 0.87, lead to population extinction.

Figure 4 shows the genetic evolution of the vector population. The histograms in the left column depict the initial distributions of mean survival time of the

vector in each phase. The graphs from top to bottom correspond to the egg, larva, pupa, and winged, respectively. In the histogram corresponding to winged stage, we can identify two maxima of the distributions that are corresponding to males (around 10) and females (around 44). In the model, the average lifespans of males and females are different. The right column shows the histograms of lifespan after 100,000 h of evolution, with 0.5 competition rate.

As the histograms indicate, after this long period, the life expectancy has been specialized at all stages of development. In the egg stage, the distribution of lifetime average now has two preferred values around 1 (12 h) and 3 (36 h) while the initial distribution

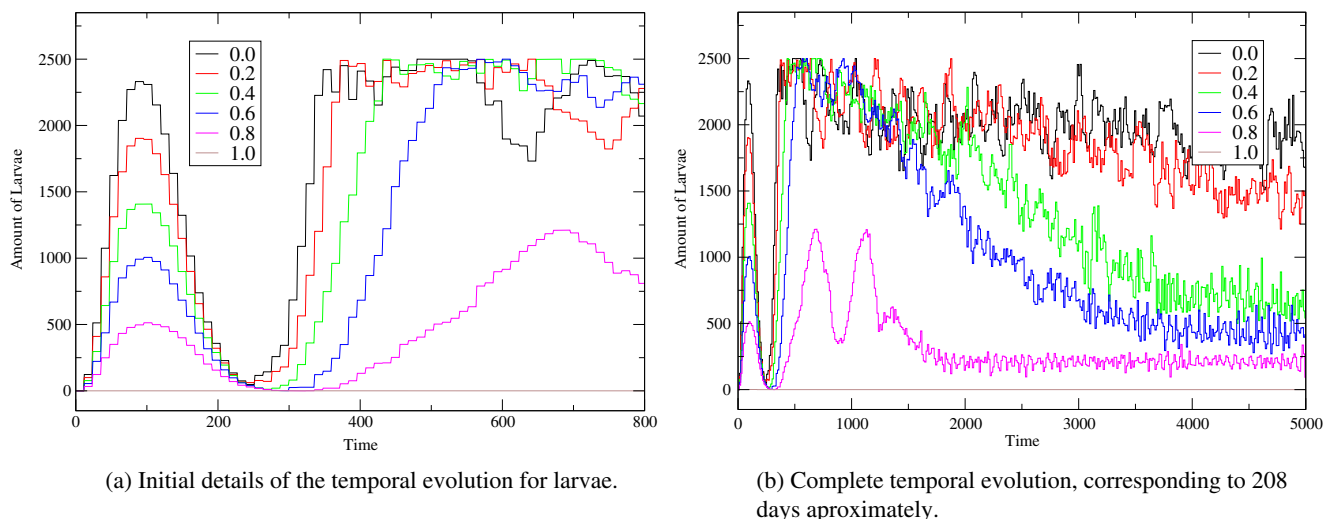


Fig. 2 Temporal evolution of larval population considering different rates of intraspecific competition

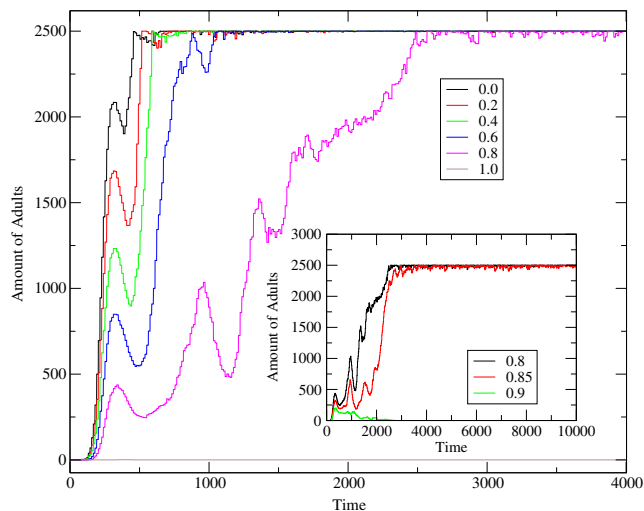


Fig. 3 Temporal evolution of the mosquitoes population for different competition rates

average was around 3. In the larval stage, the initial distribution peak around 8 (96 h) is replaced by an average around 1 (12 h). In the pupal stage, the average lifespan is also reduced. In the winged stage, by contrast, the lifespan of the females is significantly increased. In all cases, the age distribution of the vector changes.

The changes is associated with the rate of intraspecific competition: Individuals subject to external pressure tend to specialize. This effect has already been noted by Rivero et al. [7] and by Luz et al. [8], who

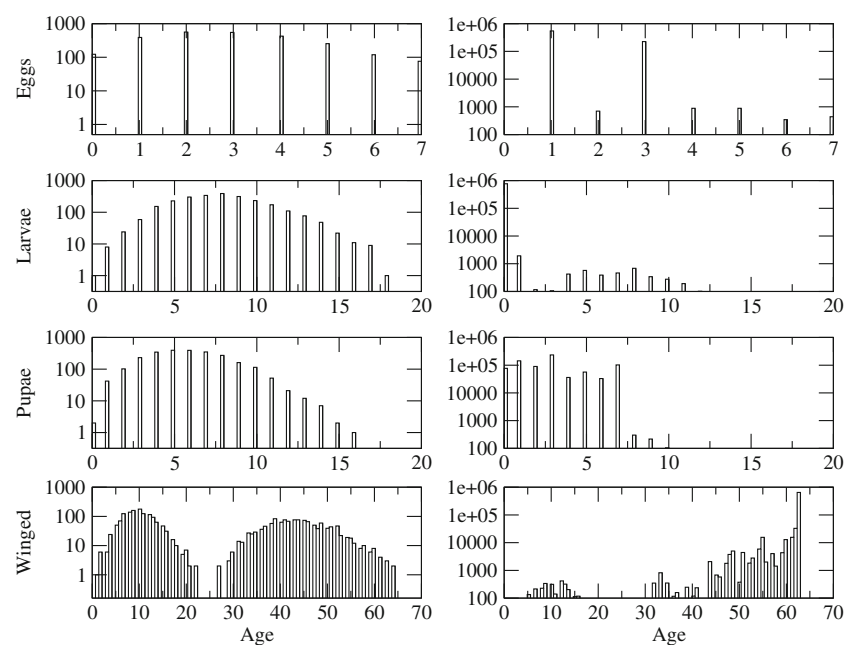
discussed the effectiveness of insecticides for vector control and showed that the insecticide affects the rate of competition. Those who survive become more resistant, which leads to specialization. Such changes are visible in the characteristics of the mosquito genomes that are represented in the histograms of Fig. 4. In our model, the genome contains information concerning the average age of individual mosquitoes during their development and reproduction. These characteristics are passed on to their offsprings, so that the influence of the competition rate making certain mosquitoes more resistant is passed to their offsprings. In the histograms, we can see that the average age of the population is altered, indicating a genetic evolution of mosquitoes as a result of competition between them.

4 Conclusion

Our results show that it is more efficient to control the population of *A. aegypti* in the larval stage, since a sufficiently high rate of intraspecific competition at this stage proved can take the entire population to extinction. This result corroborates the findings of Luz et al. [8]. Unfortunately, such high rates of intraspecific competition also trigger the evolution of the population, which adapts to new environmental conditions, as indicated by Fig. 4.

The numerical results show that the rate of intraspecific competition significantly influences the

Fig. 4 Evolution of the age distribution of the different phases of the vector population



average age at all phases of the population. Based on this, we recommend control techniques that increase competition at the larval stage, which is more sensitive than the others to high competition rates.

Regarding the evolution of the population as a whole, the changed distribution of lifetimes in Fig. 4 evidences the emergence of individuals more adapted to environmental conditions. The reduction of lifetimes in the first three phases can be understood as a gain for the vector population, since the competition is more strongly felt in these phases. On the other hand, Fig. 4 shows that adult females live longer on the average. The increased average lifespan of adults—especially that of adult females—gives them more time to produce offsprings and to generate new genetic traits. As clearly pointed out by the results, careful attention must be given to control procedures, to avoid undesirable adaptation, such as the development of resistance to certain kinds of control, of chemical control in particular [7].

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