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Seasonal and nonseasonal dynamics of *Aedes aegypti* in Rio de Janeiro, Brazil: Fitting mathematical models to trap data

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ABSTRACT

Mathematical models suggest that seasonal transmission and temporary cross-immunity between serotypes can determine the characteristic multi-year dynamics of dengue fever. Seasonal transmission is attributed to the effect of climate on mosquito abundance and within host virus dynamics. In this study, we validate a set of temperature and density dependent entomological models that are built-in components of most dengue models by fitting them to time series of ovitrap data from three distinct neighborhoods in Rio de Janeiro, Brazil. The results indicate that neighborhoods differ in the strength of the seasonal component and that commonly used models tend to assume more seasonal structure than found in data. Future dengue models should investigate the impact of heterogeneous levels of seasonality on dengue dynamics as it may affect virus maintenance from year to year, as well as the risk of disease outbreaks.

1. Introduction

Dengue fever is an arbovirosis of significant public health importance in tropical countries. Several mathematical models have been proposed since Dye's seminal work (Dye, 1984) to describe the dynamics of *Aedes aegypti*, the vector of dengue fever. Temperature and density dependent effects are ubiquitous components of those models but the way those forces are introduced differs from author to author. Validating alternative model formulations has been difficult due to the lack of long time series of mosquito data.

Honório et al. (2009a) conducted a longitudinal entomological survey with weekly collections of eggs in three neighborhoods of Rio de Janeiro, Brazil, from September 2006 to March 2008. The aim was to investigate the association between meteorological variables and mosquito density as measured by ovitraps and sticky traps (Fig. 1). The three study sites represented very distinct urban landscapes: a middle class urban neighborhood with cemented yards, paved streets and good access to water services (*Urban*); a suburban neighborhood with unpaved streets, large yards and a history of water shortage (*Suburban*); and a slum on the outskirts of the city, with unfinished houses clustered together, also with poor water supply (*Suburban Slum*). Using generalized linear models (GLM), Honório et al. (2009a) showed that mosquito density was positively and nonlinearly associated with mean air temperature (at lag 1 week) in all three neighborhoods, with expected mosquito abundance increasing linearly as temperature varied from 18 °C to 24 °C. Above this temperature threshold, mosquito abundance did not vary in response to temperature. Association with rainfall was less consistent, with only one site (*Suburban Slum*) presenting a negative association at lag 1. Lack of association between rainfall and abundance may be explained mechanistically (for example, predominance of man-filled breeding sites) or phenomenologically by lack of statistical power to detect a significant effect using regression analysis.

In this paper we revisit this dataset, this time fitting and comparing alternative mechanistic models for *A. aegypti*. GLM and mechanistic models serve different purposes. GLM models are good for identifying patterns and making short term predictions. Mechanistic models aim at explaining patterns and eventually guide intervention strategies.

A systematic review by Andraud et al. (2012) found 373 published dengue models in the English written literature, from which 42 were deterministic models using ordinary differential equations, and 28 of them had an explicit entomological dynamic model. The aim of this study was to validate a representative set of entomological models by comparing predicted and observed data. From

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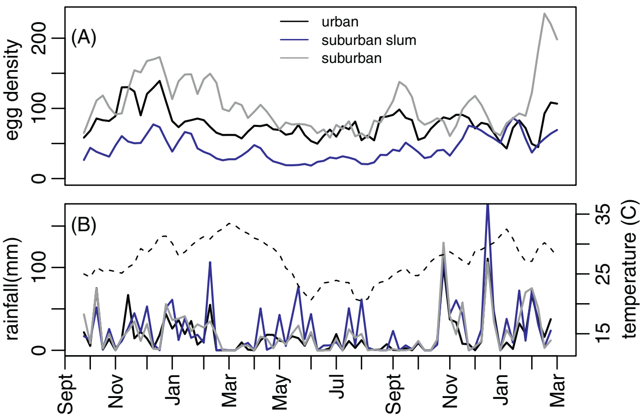

Fig. 1. (A) Time series of *Aedes aegypti* abundance measured as mean number of eggs per trap, in three neighborhoods in Rio de Janeiro, RJ, from September 2006 to March 2007. (B) The weekly time series of mean temperature (dotted line) is common to all sites; and three weekly time series of precipitation (mm), one for each neighborhood.

this, we discuss the validity of ubiquitous biological assumptions present in the dengue modeling literature and discuss the impact of the observed patterns on the dynamics of dengue fever in Rio de Janeiro.

2. Methods

2.1. Data

Entomological data come from a longitudinal survey carried out from September 2006 to March 2008 (82 weeks) in three neighborhoods of Rio de Janeiro, Brazil (22°54′S, 43°14′W). Rio de Janeiro has a tropical climate with a wet and hot summer season and a relatively dry and cool winter. This survey is fully described in Honório et al. (2009a). Each area (of approximately 500 m^2) received 40 randomly distributed ovitraps. An ovitrap is a vessel filled with an attractive infusion and a wood paddle that attracts gravid females to lay eggs. The traps were inspected every week for 82 weeks. The number of eggs per week per trap is the population index used in this study (Fig. 1A). Temperature and rainfall data from meteorological stations located no farther than 9 km from the study sites were obtained from INMET and Geo-RIO (http://www.rio.rj.gov.br/georio/alerta/tempo), respectively (Fig. 1B).

Preliminary analysis of the dataset shows that egg density is strongly autocorrelated at lag 1 week in the Suburban neighborhood and the Suburban slum, but only weakly autocorrelated in the Urban neighborhood (Fig. S1). Further inspection of the three time series (Fig. 1) shows that the latter is the one with least evidence of seasonality as well. Finite rate of population increase was calculated as lambda = log(Egg(week + 1)/Egg(week)). The linear decrease of lambda in response to density in all three neighborhoods (Fig. S1) is consistent with the hypothesis of density-dependent population regulation.

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2.2. Mathematical models

A. aegypti is a container breeding mosquito that lays eggs on the inner wall of water filled containers. Eclosion is triggered by complex environmental drivers, which combine abiotic (humidity, temperature) and biotic signals (presence of larvae) (Livdahl and Edgerly, 1987). Newborn larvae feed on detritus and microorganisms present in the water until they achieve sufficient physiological conditions for pupation (Christophers, 1960). Growing larvae compete for resources in a spatially limited environment and experimental studies have shown that crowding and resource limitation is associated with high larval mortality, increased time to maturity, weaker adults and lower fecundity (Moore and Fisher, 1969; Mulla, 1979; Southwood et al., 1972). Emerging adult females copulate and spend their lives between blood feeding and egg maturation and ovipositing activities (Christophers, 1960). Ovipositing is density-dependent as female choice is affected by the presence of eggs (Chadee, 2009) and larvae (Zahiri and Rau, 1998). Oviposition behavior is further affected by the physical–chemical characteristics of the breeding sites (Bentley and Day, 1989; McCall and Cameron, 1995). Death occurs mostly by density-independent events (predation, insecticide) (Bar-Zeev, 1958; Christophers, 1960; Rueda et al., 1990), although recent studies suggest that mosquitoes may also senesce (Bellan, 2010; Harrington et al., 2008).

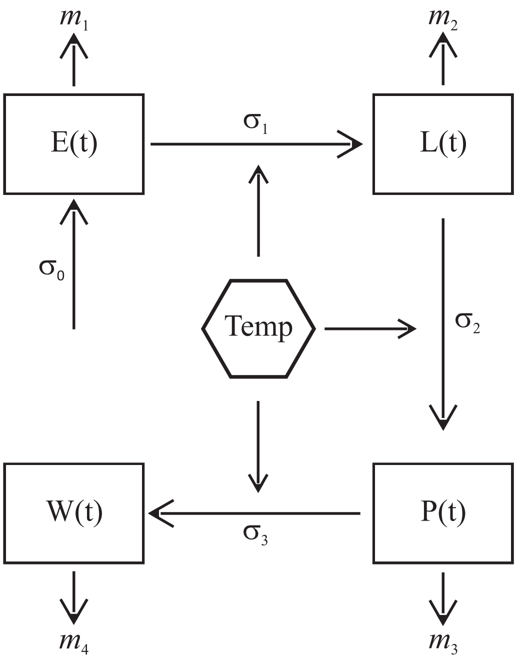

Fig. 2. Diagram showing the *Aedes aegypti* population model with four compartments: egg, larvae, pupae and adults. σ_s represent the temperature-dependent development rates: σ_1 – egg to larva, σ_2 – larva to pupa, and σ_3 – pupa to adult. σ_0 is the oviposition rate; K is the carrying capacity; m_1, m_2, m_3 and m_4 are the stage-specific death rates.

Most authors synthesize this complex life history into variations of an Egg → Larva → Pupa → Adult linear transition model (Fig. 2). Four differential equations describe the flow of individuals between stages (Eq. (1)), where σ are the transition rates and m are the mortality rates. Eq. (1a) describes the variation in egg density, which increases with oviposition and decreases with eclosion and mortality. Eq. (1b) describes the larval population that increases with egg eclosion and decreases with mortality and pupation. The pupal population (Eq. (1c)) increases with pupation and decreases with mortality and adult emergence. Finally, the adult compartment (Eq. (1d)) increases with emergence and decreases with mortality. This model presents unstable dynamics unless a density-dependent term is introduced.

$$\frac{dE}{dt} = \sigma_0 W - [\sigma_1 + m_1]E \tag{1a}$$

$$\frac{dE}{dt} = \sigma_1 E - [\sigma_2 + m_2]L \tag{1b}$$

$$\frac{dE}{dt} = \sigma_2 L - [\sigma_3 + m_3]P \tag{1c}$$

$$\frac{dE}{dt} = \sigma_3 P - m_4 W \tag{1d}$$

We implemented variations of this model, combining features from different published models that describe the population dynamics of *A. aegypti*. They differ in how the temperature-dependent development rate and the density-dependent population regulation are represented. We further considered models with constant carrying capacity and models with time varying carrying capacity. Candidate models were restricted to ordinary differential equation models, which are components of most dengue models. Other classes of *A. aegypti* models include individual-based models such as Focks et al. (1993a). Those models require more input information than what was available and the number of free parameters greatly exceed the number of observed data points.

2.2.1. Temperature-dependent transition rates

There is no controversy regarding the importance of temperature on the development of *A. aegypti*. However, models differ in the way temperature-dependent transition rates are implemented. For example, Ferreira and Yang (2003a) use a three step function, while Yang et al. (2009) use polynomial functions derived from empirical data. Focks et al. (1993a) and Otero et al. (2006) use a mechanistic representation, the thermodynamic equation (Otero et al., 2006). Luz et al. (2009) use sinusoidal functions to mimic temperature seasonal variations.

Two types of temperature-dependent transition rates were introduced to create extensions of the basic model (Eq. (1)). The goal was to compare and assess the sensibility of the model to alternative functions present in the literature. The first one is the three-step function adapted from Ferreira and Yang (2003a) where the transition rates assume one of three fixed values, depending on the mean air temperature (Table 1):

if

$$\begin{aligned} &T < 22\,^{\circ}\mathrm{C} = \sigma_{il} \\ &22\,^{\circ}\mathrm{C} <= T <= 26\,^{\circ}\mathrm{C} = \sigma_{im} \\ &T > 26\,^{\circ}\mathrm{C} = \sigma_{ih} \end{aligned} \tag{2}$$

The rationale is that in tropical cities, time periods can be divided in favorable or unfavorable conditions for mosquito development according to the mean air temperature. If air temperature is below 22 °C, development is retarded, taking an average of 11 days for a larva to evolve to pupa. This is in accordance with field experiments performed near the study area which show that under this temperature regime, larvae would still be between the second and third stage after 7 days since eclosion (Câmara et al., unpublished results). As temperature increases, the function predicts a stepwise increase in developmental rate. Faster development at higher temperatures (up to 35 °C) is supported by laboratory data (Yang et al., 2009), but contradicts observational data. Experimentally colonized artificial containers in Rio de Janeiro showed reduced development at temperatures above 28 °C (Câmara et al., unpublished results).

The second function is the thermodynamic equation (Eq. (2)) parameterized for *A. aegypti* (Focks et al., 1993a; Otero et al., 2006). This function describes the kinetics of a single enzyme that is activated within a temperature range and deactivated outside this range. Within the temperature range observed in Rio de Janeiro, this function produces an almost linear relationship between development and temperature.

$$\sigma_i = \sigma \frac{(T/298)\exp((a_i/R)(1/298 - 1/T))}{1 + \exp(b_i/R)(1/T_{1/2} - 1/T)} \tag{3}$$

where T is the mean weekly temperature, measured in Kelvin, and a_i, b_i are specific parameters for each life-history stage i (Table 1); R is the universal gas constant.

2.2.2. Density-dependent effects

Esteva and Yang (2005), Ferreira and Yang (2003a) and Massad et al. (2010) introduce density-dependence in the per capita oviposition rate, Dye (1984) and Luz et al. (2009) implement it in the survival rate of the larval stage. Magori et al. (2009), on the other hand, implements a simulation model where density dependence acts on larval survival and pupal weight.

In this study, density-dependence regulation was introduced either in the oviposition rate (Ferreira and Yang, 2003a) or in the egg hatching rate (Otero et al., 2006) in the form of a logistic function. Respectively:

$$\sigma_0 = \sigma_0^{\max}\left[1 - \frac{E}{K}\right] \tag{4}$$

or

$$\sigma_1 = \sigma_1^{\max}\left[1 - \frac{L}{K}\right] \tag{5}$$

where K is the carrying capacity and ${\sigma_0}^{\max}$ is the maximum oviposition rate and ${\sigma_1}^{\max}$ is the maximum eclosion rate. Formulations using generalized logistic functions were also assessed, but since goodness-of-fit was not improved, those results are not shown.

Table 1
Symbols used in the models and their values.

Parameter	Value	References
Oviposition rate (σ_0)	1.0 day^{-1}	Ferreira and Yang (2003a)
Develop. rates: step function models		
Egg eclosion rate (σ_1)	$(l, m, h) = (1/4.5, 1/3.3, 1/2)\,\mathrm{day}^{-1\,\mathrm{a}}$	
Pupation rate (σ_2)	$(l, m, h) = (1/11.7, 1/8, 1/4.4)\,\mathrm{day}^{-1\,\mathrm{a}}$	Ferreira and Yang (2003a)
Emergence rate (σ_3)	$(l, m, h) = (1/4.6, 1/3.1, 1/6)\,\mathrm{day}^{-1\,\mathrm{a}}$	
Develop. rates: kinetics function models		
Egg eclosion rate (σ_1)	$\sigma(298), a_i, b_i, T_{1/2} = (0.24, 10798, 100000, 14184)^{\mathrm{b}}$	Sharpe and DeMichele (1977), Schoofield et al. (1981) and Focks et al. (1993a)
Pupation rate (σ_2)	$\sigma(298), a_i, b_i, T_{1/2} = (0.2088, 26018, 55990, 304.6)^{\mathrm{b}}$	
Emergence rate (σ_3)	$\sigma(298), a_i, b_i, T_{1/2} = (0.384, 14931, -472379, 148)^{\mathrm{b}}$	
Egg mortality rate (m_1)	1/100 day^{-1}	
Larva mortality rate (m_2)	1/3 day^{-1}	
Pupa mortality rate (m_3)	1/70 day^{-1}	Ferreira and Yang (2003a)
Adult mortality rate (m_4)	1/17.5 day^{-1}	
Carrying capacity (K)	Fitted eggs/trap/week	–

[*] l, lower rate; m, intermediate rate; h, higher rate.

[**] Units: σ is measured in day^{-1}, a_i and b_i is measured in cal/mol and T is measured in Kelvin degrees.

Models with density-dependent larval mortality also exist in the literature (Luz et al., 2009). Our data (number of laid eggs), however, does not allow discrimination between a model with density dependent egg eclosion (Eq. (4)) and density dependent larval mortality (non-identifiability).

2.2.3. Time-varying carrying capacity

The carrying capacity, K, was initially considered as a time-unvarying parameter. Subsequent formulations allowed temporal variation by partitioning the data time window into k parts and calibrating K separately for each one ($k = 2$ through $k = 6$ partitions were tested). Larger partitions could not be tested because the time series is small. A seasonal function was also investigated, with $K(t)$ following a sinusoidal function with a 1-year period. A Fourier decomposition of the rainfall data showed a strong signal at this frequency (data not shown).

2.2.4. Candidate mathematical models

The combination of temperature and density functions described above led to four models, named *TSE*, *TSL*, *TCE* and *TCL*.

TSE: temperature dependent step function + density-dependent oviposition (Eq. (3) + Eq. (4))
TCE: thermodynamic function + density-dependent oviposition (Eq. (2) + Eq. (4))
TSL: temperature dependent step function + density-dependent larval development (Eq. (3) + Eq. (5))
TCL: thermodynamic function + density-dependent larval development (Eq. (2) + Eq. (5))

Versions of those models with time-varying K are referred to as *model_t*(k), where k is either the number of steps ($k = 2$–6) or $k = s$ if K follows a sinusoidal function.

2.3. Model calibration and model selection

Candidate models were simulated and calibrated using TerraME, an open source programming environment for spatial dynamical modeling (http://www.terrame.org, Carneiro et al., 2013). All parameters but K (the carrying capacity) received values from the literature (Table 1). Only K, which measures the unknown amount and quality of available breeding sites, was defined as a free parameter to be calibrated using the data. For each study area, two egg time series were created, each one calculated as the mean number of eggs per trap, averaged over half of the 40 available traps. The rationale was to generate two independent datasets for each area, one for fitting, and the other for validation.

Before calibration, egg density time series were smoothed using a moving average filter with window 3. Calibration was carried out using a genetic algorithm with automatic parameter update, implemented in TerraME (Pedrosa Silva et al., 2011). Model output used for calibration was the number of eggs laid in a week: $\int \sigma_0(t) W dt$. Goodness-of-fit was measured by *AIC*, and by the linear correlation between predicted and observed values (*Pearson* and *Spearman*). The difference in *AIC* of each model in comparison to the model with the lowest *AIC* ($\Delta(AIC)$) (Spiess and Neumeyer, 2010), was also calculated to facilitate comparison. Moreover, the autocorrelation structure of residuals was investigated as well as their correlation with temperature, precipitation and the population's finite rate of increase.

All analyses and graphs were performed using R 2.14 (R Development Core Team, 2011).

3. Results

3.1. Comparison of models TSE, TSL, TCE and TCL

Fig. 3 shows the best fit curves generated by the four models with constant K. Overall, all models predicted higher mosquito

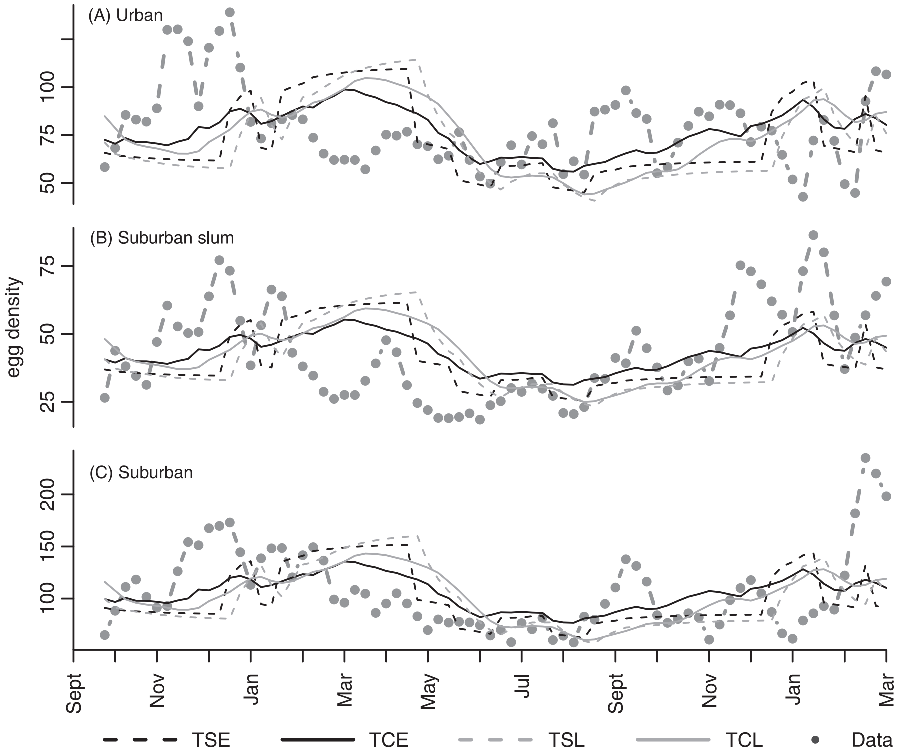

Fig. 3. Observed and predicted *Aedes aegypti* time series for the three neighborhoods in Rio de Janeiro, RJ, according to the four models with fixed K. See text for the description of the models: *TSE*, *TCE*, *TSL* and *TCL*.

Table 2
Goodness-of-fit of *TSE*, *TSL*, *TCE* and *TCL* models to the ovitrap data of three neighborhoods of Rio de Janeiro.

Site	Urban				Suburban				Suburban Slum			
Model	TSE	TSL	TCE	TCL	TSE	TSL	TCE	TCL	TSE	TSL	TCE	TCL
AIC	736.75	749.46	696.05	724.92	787.44	798.62	760.41	777.41	657.25	684.85	642.99	658.90
ΔAIC	40.70	53.40	0.00	28.87	27.03	38.21	0.00	17.00	14.26	41.86	0.00	15.91
Spearman (%)	−3.03	−11.43	1.30	−14.08	37.98	29.52	43.45	28.76	15.70	−5.27	32.87	10.65
Pearson (%)	−8.77	−20.99	2.52	−9.94	20.71	11.44	36.18	23.72	25.94	−9.47	32.19	15.09

abundance during the summer and fall months (January to May), failing to detect the already high mosquito abundance observed during the spring, especially in the first year, in all neighborhoods. Spring in Rio de Janeiro is characterized by average temperatures ranging from 23° to 26° C, a temperature range to which *A. aegypti* development is very sensitive (Riback et al., unpublished results).

Among the four models, *TCE* consistently presented the lowest *AIC* while the *TSL* presented the highest (Table 2). *TCE*'s goodness-of-fit varied between neighborhoods, being moderate in the Suburban slum and Suburban neighborhoods (correlation = 0.33 and 0.43, respectively) and very poor in the Urban neighborhood ($r = 0.013$). The residual analysis provided further clues regarding the models' behavior. Fig. S2 shows the residual autocorrelation plot and Figs. S3–S5 show the generalized additive regression of residuals × temperature. The Suburban slum was the area where residuals were least structured, with no significant autocorrelation or association with temperature. This was also the area with stronger climate dependent signal (Honório et al., 2009a). The Urban neighborhood is in the other extreme. Mosquito abundance showed weak autocorrelation (Fig. S1) and weaker association with temperature (Honório et al., 2009a) as compared to the other neighborhoods. Since the mathematical models assume strong temperature dependence (seasonality), residuals appeared autocorrelated and strongly associated with temperature. In other words, there is more structure in the residuals than in the data itself. The Suburban neighborhood is an intermediate scenario.

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Residuals also correlated with the population's finite rate of increase, although less strongly than the original data (Fig. S1) (residual × lambda linear regression's $R^2 = 5–10\%$).

3.2. Models with time-varying carrying capacity

Table 3 and Fig. 4 show the goodness-of-fit of models with time-varying carrying capacity. We present the results of the *TCE_t* model only, the one with the best fit. In all neighborhoods, the time-varying *K* models provided a better fit, what was expected as the number of free parameters increased. The best models were those with $k = 4$ (in the Suburban slum, with Spearman $r = 0.51$), and $k = 6$ (in the Urban and Suburban areas, with $r = 0.63$ and 0.75, respectively). It is interesting to note the relatively poorer performance of the model with sinusoidal carrying capacity in the urban and suburban neighborhoods, according to *AIC* and correlation coefficients (Table 3). One possible explanation was the distinct carrying capacities recorded in the two summer seasons in the suburban neighborhood and the poor seasonal signal observed in the urban neighborhood. These patterns are not well described by the rigid structure of the sinusoidal function. In the suburban slum, on the other hand, the sinusoidal model was almost as good as the *TCE* model.

Fig. 5 shows the estimated time-varying carrying capacity in the three neighborhoods, according to *TCE_t*(6). Overall, the smallest carrying capacity was measured in the Suburban slum ($K = 115–248$), followed by the Urban neighborhood ($K = 285–550$) and the Suburban neighborhood ($K = 381–676$). In all areas, carrying capacity was high in the spring of 2006 and during the winter of 2007. After this winter, neighborhoods differed, with the Urban neighborhood presenting low *K* in the following spring–summer, the Suburban neighborhood reaching a high plateau in the summer and the Suburban slum presenting high values during the spring and summer. No direct correlation was observed between *K* and precipitation (Fig. 5).

4. Discussion

Tropical mosquito population abundance is controlled by exogenous (environmental) and endogenous (density-dependent) drivers. The relative contribution of each component may differ between species and between environments (Yang et al., 2008). In this study, we considered a family of mathematical models with density-dependence and environment-dependent factors (temperature) that are commonly hypothesized for *A. aegypti*. Those models produce abundance curves that vary seasonally around an average value controlled by the environmental carrying capacity.

Table 3
Goodness-of-fit of the *TCE* model with time varying carrying capacity *K*.

Model # Parameters	TCE_(1) 1	TCE_(2) 2	TCE_(3) 3	TCE_(4) 4	TCE_(5) 5	TCE_(6) 6	TCE_(s) 3
Urban							
AIC	696.05	697.75	697.44	658.11	666.90	643.83	671.31
Spearman (%)	1.30	0.27	5.77	47.32	45.29	51.48	38.56
Pearson (%)	2.52	−0.77	2.90	54.17	47.67	66.37	37.46
Suburban							
AIC	760.41	758.27	757.71	749.49	755.67	**741.34**[a]	758.79
Spearman (%)	43.45	51.16	51.30	59.97	54.28	**63.00**	51.06
Pearson (%)	36.18	43.69	47.49	55.43	51.52	**63.75**	45.36
Suburban Slum							
AIC	642.99	631.71	619.36	**592.12**[a]	602.13	603.69	602.91
Spearman (%)	32.87	52.18	59.21	**75.45**	72.93	73.35	72.51
Pearson (%)	32.19	51.95	62.45	**75.64**	72.43	72.62	70.53

[a] Best fit models in bold.

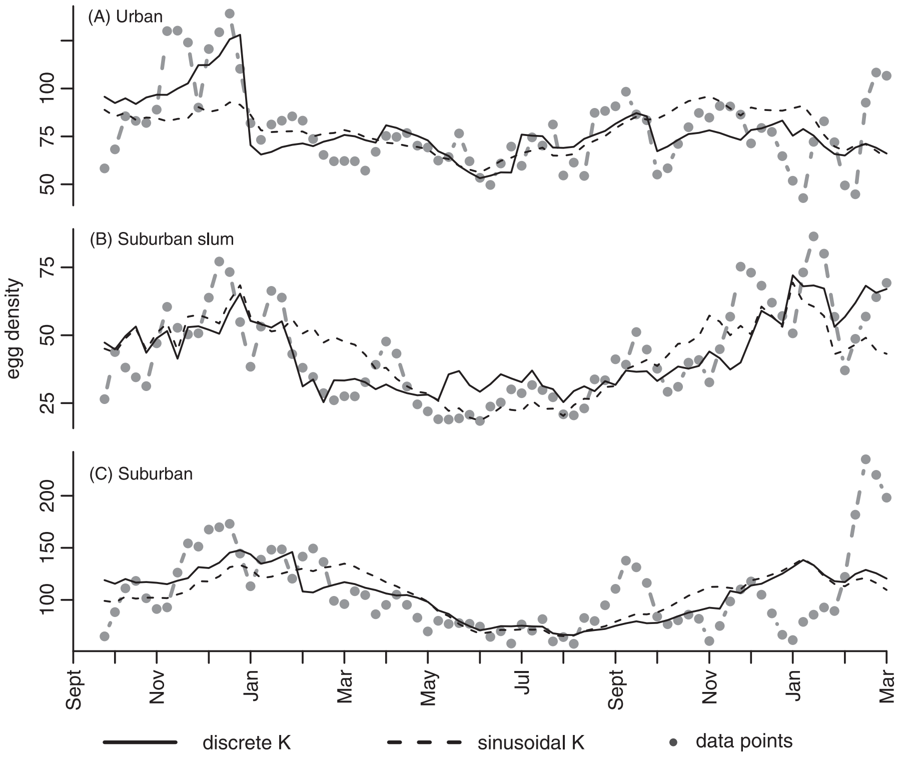

Fig. 4. Observed and predicted *Aedes aegypti* time series for the three neighborhoods in Rio de Janeiro, RJ, according to the *TCE* model with 6 values of *K* (*TCE_t*(*k* = 6)) and the sinusoidal model (*TCE_t*(*s*)). See text for the description of the models.

Previous analysis of this dataset using regression analysis indicated a strong nonlinear association with temperature and a strong autoregressive component (Honório et al., 2009a). These are standard assumptions of mechanistic models broadly used as tools to derive optimal vector control strategies for *A. aegypti* and predictions for dengue dynamics. By fitting those models to *A. aegypti*'s abundance in Rio de Janeiro, Brazil, we found, however, that models assume more seasonality and density-dependence than was observed, in two of the areas. This became evident in the analysis that showed residuals with more autocorrelation structure than the data itself in the Urban and Suburban neighborhoods.

The best fit model, *TCE_t*(6), assumes a continuous temperature-dependent developmental rate, a density-dependent oviposition rate and a different value for the carrying capacity at every 3–4 months. The better performance of the continuous temperature dependent function is consistent with the biological literature. Laboratory experiments where development time is recorded at constant temperature regimes show that the rate of development increases almost linearly between 19 and 34 °C. Still this continuous function (*TCE* and *TCL*) produced outputs that were very smooth, failing to capture the peaks and valleys present in the mosquito time series. The *TSE* and *TSL* models (with the step temperature function), on the other hand, generated rougher outputs but again failed to fit the observed ups and downs. There is a periodicity in the data set, characterized by a period of ca. 2 months that is not captured by any of the candidate models, suggesting that other factors may be modulating this dynamics.

Inclusion of density-dependence in the oviposition term resulted in a slightly better fit than in the larva equation. The literature presents contradictory support to the density-dependent

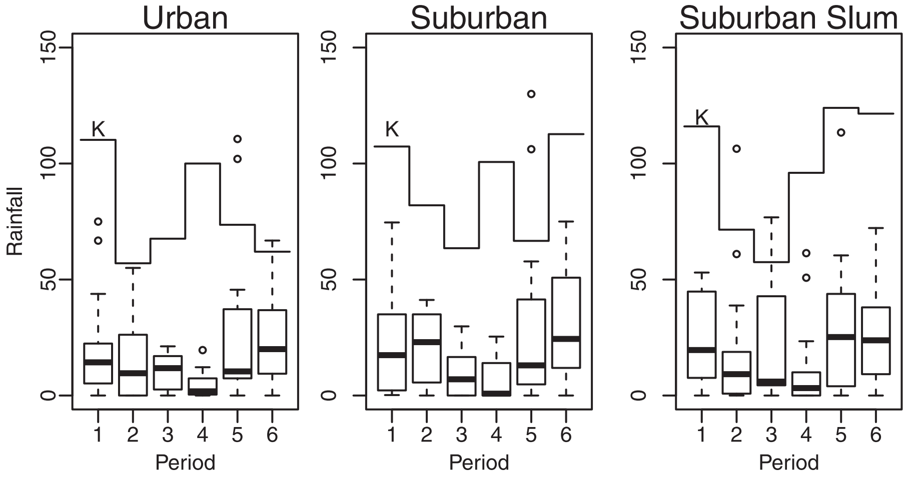

Fig. 5. Estimated carrying capacity according to the model *TCE_t*(6) and boxplots of weekly precipitation at 12-week intervals in three neighborhoods of Rio de Janeiro, Brazil.

oviposition. Allan and Kline (1998) report a two choice experiment were the oviposition response of gravid *A. aegypti* was compared between an oviposition paper containing preexistent eggs and no eggs, showing preference for the former. On the other hand, Chadee et al. (1990) argue that a gravid female can only predict the number of larvae that will share habitat with its offspring by assessing the number of eggs, and they found experimentally, that gravid females prefer to oviposit in pots, which were not visited by themselves or co-specifics. The response of gravid females to eggs is supported by the presence of semiochemicals from egg origin that act as stimulant or inhibitor of oviposition behavior (Ganesan et al., 2006). More research is necessary to bring more information to this subject.

Recent re-analysis of the seminal life table data by Southwood et al. (1972) that inspired most *A. aegypti* models suggested that mathematical models tend to deemphasize the importance of density independence mechanisms while emphasizing density dependence. A better understanding of the role of density-dependent and independent forces on the regulation of *A. aegypti* is fundamental for the proper understanding and evaluation of vector control strategies (Legros et al., 2009).

Rio de Janeiro is a tropical megalopolis, characterized by climate conditions that favor the maintenance of *A. aegypti* population year-round. Ovipositing activities of *A. aegypti* are detected in more than 50% of the households even during the winter (Honório et al., 2009a). During the summer of 2007, more than 90% of traps detected oviposition. The Suburban slum was the area with the lowest mosquito population abundance and the strongest seasonality. This is a densely human populated area at the outskirts of the city where large amounts of garbage accumulate outdoors. Exposure to weather and absence of intense vector control activities in that area provide the ideal scenario for the mathematical models discussed here. In this area, the best model was *TCE_t*(4), which identified higher carrying capacity during the summer and winter months. High carrying capacity during the winter can be associated with water storage during the dry season or increased attractiveness of ovitraps during this season. This neighborhood was the only one where the model with sinusoidal carrying capacity performed almost as well as the best model (Table 4), with a Pearson correlation of 70%. This model, despite its structural rigidity, presented better fit than a GLM (Honório et al., 2009a).

Contrastingly, the *Urban* neighborhood presented high mosquito abundance with weak seasonal variation. Although correlation between temperature and abundance do exist (Honório et al., 2009a), as well as density dependence (Fig. S1), they were less significant than those expected by the model's assumptions, and the resulting model predicted a seasonality that was not present in the data. One possible explanation for this weak response of mosquitoes to climate in the Urban neighborhood could be the predominance of indoor breeding sites. Most premises in this area had clean yards with no cluttering, main breeding sites taking the form of man-filled containers such as flower pots (Honório, personal observation).

Finally, the Suburban neighborhood presented an intermediate scenario. This area has houses with large peridomestic areas and unpaved streets. In addition, breeding sites were commonly found outdoors and took the form of large containers such as boat hulls, metal drums and water tanks (Maciel-de-Freitas et al., 2007). The best model, *TCE_t*(6), captured the temperature-driven seasonality well, which was less marked than in the Suburban slum. The carrying capacity had high and low values occurring in all seasons.

Overall, our results suggest that the population dynamics of *A. aegypti* vary from strong to weak seasonality within the large and heterogeneous city that is Rio de Janeiro. Luz et al. (2003) developed a dengue model for Rio de Janeiro to investigate the impact of mosquito spatial heterogeneity on dengue R_0. They stressed the increased risk associated with maintaining highly infested areas in central parts of the city, which contribute largely to the city-level mean transmission risk. The Urban area studied here represents such a high-risk area due to its high carrying capacity, weak seasonality, and centrality within the city.

Despite the strong seasonality of dengue fever notifications in Rio de Janeiro (Luz et al., 2008), transmission does occur year-round (Honório et al., 2009b). Large pockets of mosquito populations during the winter in some localities may contribute to the maintenance of the virus population from year to year. Multi-strain dengue models have shown that complex chaotic dynamics may emerge more commonly in scenarios with strong seasonality in comparison to scenarios with no seasonality (Aguiar et al., 2011). They did not investigate spatial heterogeneity, though. Future dengue fever models should investigate the impact of heterogeneous levels of seasonality on dengue fever dynamics.

Conflict of interest

The authors declare that there is no conflict of interest.

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