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Análise Temporal da Dinâmica do Mosquito da Dengue (*Aedes aegypti*) em Porto Alegre, Rio Grande do Sul

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Análise Temporal da Dinâmica do Mosquito da Dengue (*Aedes aegypti*)

em Porto Alegre, Rio Grande do Sul

Guilherme Barradas Mores

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Resumo

O controle do mosquito *Aedes aegypti* é importante para evitar que milhões de pessoas contraiam arboviroses e é um desafio aplicado de Ecologia de Populações. Porém há uma distancia grande entre os estudos com *A. aegypti* e a abordagem moderna de análise de populações, a modelagem hierárquica de parâmetros populacionais. Realizei este trabalho visando promover o maior uso desta abordagem no estudo do *A. aegypti.* Ajustei um modelo da dinâmica intra-anual da infestação por *A. aegypti* em Porto Alegre, Rio Grande do Sul, Brasil utilizando dados de quatro anos de monitoramento entomológico semanal por uma rede de centenas de armadilhas para adultos. Em seguida usei análise de sensitividade para inferir qual o melhor período do ano para aplicação de controle. A infestação variou de quase todos os lugares infestados nos meses de verão, a aproximadamente 10% infestados no inverno. Contudo, a maior sensitividade ao controle foi encontrada no outono. Acredito que este trabalho tem resultados práticos para ser aplicado no combate a arboviroses em Porto Alegre, mas também seja inspirador para que mais pessoas usem modelagem hierárquica de parâmetros populacionais no estudo do *A. aegypti.*

Palavras chaves: Ecologia de Vetores, Modelo Dinâmico, Demografia, Dengue, Zika, Cidade Subtropical, Ocupação de Sítios

Abstract

The control of the *Aedes aegypti* mosquito is important both to avoid arboviral disease transmission to millions of humans and as an applied challenge in Population Ecology. However, there is a great gap between studies with *A. aegypti* and the modern approach to population analysis, the hierarchal modeling of population parameters. I developed this work with the aim of promoting a greater use of this approach in *A. aegypti* studies. I fitted a model of intra-annual infestation dynamics by *A. aegypti* in Porto Alegre, Rio Grande do Sul, Brazil, using four years of weekly entomological monitoring data obtained with a network of hundreds of adult traps. Next, I used sensitivity analysis to infer what is the best period of the year to apply mosquito control. Infestation varied from almost all sites infested in summer months, to nearly 10% infested in winter; however, greater sensitivity to control was found during the autumn months. I believe this work has relevant practical implications in the fight against arboviral diseases in Porto Alegre, and hope that it can inspire more people to apply hierarchal modeling approaches in the analysis of *A. aegypti* populations.

Keywords: Vector Ecology, Dynamic Model, Demography, Dengue, Zika, Subtropical City, Site Occupancy

Sumário

Introdução geral

O mosquito da dengue (*Aedes aegypti*) é um fator de risco para a saúde publica a nível global[1]. Ele é o vetor de várias arboviroses que infectam milhões de pessoas todos anos. A principal arbovirose é a Dengue,[2] que, por ano, afeta 58 milhões de pessoas e causa 10 mil mortes. A maior parte dessas arboviroses não tem uma vacina amplamente funcional, incluindo a Dengue.[3] Por tanto, manter a abundância do mosquito suficientemente baixa para evitar a transmissão é a melhor forma de prevenir as arboviroses.

O controle do *A. aegypti* pode ser visto como um desafio prático de Ecologia de Populações. Conhecendo os processos que controlam a distribuição e abundância do mosquito é possível não só prever onde e quando haverá maior risco de transmissão, como averiguar e prever o efeito de diferentes técnicas de controle. Como as populações do *A. aegypti* variam anualmente de forma diferente dependendo de fatores ambientais,[4] principalmente precipitação e temperatura, também é possível identificar locais semelhantes quanto a dinâmica do mosquito, onde resultados obtidos em um local seriam mais facilmente replicados em outro.

A Ciência do controle de *A. aegypti* foi majoritariamente praticada por médicos e veterinários, o que criou um distanciamento do resto da Ecologia. Esta distância fica clara principalmente comparando os princípios de amostragem, apesar de já existirem aproximações.[5] Os ecólogos de populações têm buscado se afastar de calcular índices, para estimar diretamente parâmetros populacionais.[6] Estas estimativas são preferencialmente feitas através de uma sepração formal entre o processo de amostragem e da dinâmicas populacional. Esta abordagem, que pode ser descrita como modelagem hierárquica de parâmetros populacionais, permite comparações entre resultados obtidos de diferentes técnicas de amostragem, com a incerteza quanto às estimativas explicitamente expostas.

No monitoramento do mosquito da dengue ainda há a premissa, ainda que implicita, que o processo biológico e de amostragem não pode ser separado. Por exemplo, numa revisão recente sobre controle integrado de vetores,[7] as técnicas de amostragens apresentadas são acompanhadas de seu índice entomológico específico. Apesar de já ter sido útil, esta abordagem dificulta a comparação entre resultados obtidos com diferentes técnicas de amostragens, além de ser suscetível a vieses causados pela amostragem e de não produzir uma medida explicita de incerteza. Além disso um índice pode indicar se uma população em um lugar é maior ou menor que noutro lugar, porém não o número real de indivíduos. Uma estimativa de abundância real é muito mais interessante do ponto de vista prático, já que pode ser utilizada para calcular, por exemplo, a razão entre humanos e mosquitos, fator importante na modelagem de epidemias.[8]

Minha motivação para a realização deste trabalho foi esta necessidade da amostragem do *A. aegypti* incorporar conceitos de amostragem da Ecologia de Populações. Eu acredito que, para esta incorporação acontecer, pesquisadores e tomadores de decisão sobre o mosquito da dengue devem tomar conhecimento de trabalhos que, usando estes conceitos, cheguem a resultados confiáveis e interessantes. Na esperança de fazer um destes trabalhos, modelei a população do mosquito da dengue em Porto Alegre com base em dados de monitoramento entomológicos da Prefeitura Municipal. Meu objetivo foi primeiramente descrever a dinâmica anual da população, para que posteriormente cidades parecidas com ela possam obter resultados comparáveis. Depois, usei a técnica de analise de sensitividade[9] para investigar qual o momento ideal do ano para se aplicar controle epidemiológico.

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Capitulo 1:Site occupancy by *Aedes aegypti* in a subtropical city is most sensitive to control during Autumn months[1]

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KEYWORDS:

Site occupancy, Sensitivity analysis, Mosquito control, Population fluctuation

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[1] Este capitulo corresponde a um artigo submetido ao American Journal of Tropical Medicine and Hygiene. A formatação foi levemente modificada para facilitar a leitura.

ABSTRACT

The *Aedes aegypti* mosquito inhabits most tropical and subtropical regions of the globe where it transmits arboviral diseases of substantial public health relevance, such as Dengue fever. In subtropical regions, *A. aegypti* often presents an annual abundance cycle driven by weather conditions. Because different population states may show varying responses to control, we are interested in studying what time of the year is most appropriate for control. To do so, we developed a dynamic site-occupancy model based on more than 200 weeks of mosquito-trapping data from nearly 900 sites in a subtropical Brazilian city. Our phenomenological, Markovian model, fitted to data in a Bayesian framework, accounted for failure to detect mosquitoes in sites where they actually occur and for temporal variation in dynamic rates of local extinction and colonization of new sites. Infestation varied from nearly full cover of the city area in late summer, to approximately 10% of sites occupied in winter. Sensitivity analysis reveals that changes in dynamic rates should have the greatest impact on site occupancy during the Autumn months, when the mosquito population is declining. We discuss the implications of this finding to the timing of mosquito control.

INTRODUCTION

Control of the mosquito and disease vector *Aedes aegypti* is an important public health challenge.[1] Originated from Africa and unintentionally dispersed by humans around the world, *A. aegypti* is currently present in tropical and subtropical regions of Africa, Asia, Oceania and the Americas.[2] It is well adapted to urban environments because it can breed in artificial water containers and feed on human blood.[2] Although dormant eggs can survive unfavorably cold and dry seasons, the survival, growth and reproduction of the other life stages is dependent on rainy and hot weather.[3] Thus, *A. aegypti* populations present high year-round abundances in tropical humid regions and annual cycles of abundance in most other regions where the species occurs.[3] When sufficiently abundant, *A. aegypti* is a vector of many disease-causing arboviruses, including Chikungunya,[4] Zika,[5] Yellow fever[6] and Dengue fever.[7] Dengue fever is of particular concern since it is the most common human arboviral disease.[8] More than one third of the world population is at risk of contracting Dengue,[9] with yearly numbers of 58 million people infected, 10 thousand deaths, and 1.14 million DALY (Disability Adjusted Life Years) lost due to the disease.[8] With no universal vaccine for Dengue available, vector control is still the most reliable way to prevent epidemics.[10]

Since the 1970's, control of *A. aegypti* has relied mostly on ultra-low volume insecticide spraying and community-based removal of breeding sites.[7] However, with all the effort that has been spent on control, the number of people infected by the disease is still increasing, doubling every 10 years since 1990.[8] Brazil and Mexico, for example, have not managed to contain the disease despite spending yearly amounts of, respectively, US$ 450 million[11] and US$83 million[12] during the last decade. The growth of Dengue incidence over the last forty years makes it clear that vector control has been insufficient.[13] Acknowledging the need to improve vector control, the scientific community and public health agencies routinely discuss existing and potential control strategies.[10,14,15] These discussions usually emphasize development and introduction of new control methods, such as biocontrol, sterile male release or genetic-modifications that render mosquitoes incapable of transmitting Dengue.

Our interest here is not on how but when to apply control measures: an aspect of control planning that is easily overlooked. Appropriate timing matters regardless of the method of choice and requires knowledge of mosquito population dynamics. Control interventions applied in distinct moments of a mosquito's annual population cycle may result in very different consequences, with modeling results suggesting that intervening when abundance reaches above a threshold may not be the optimal strategy.[16] Applying control permanently is budget intensive and may lead to evolution of resistance on the mosquito population. Researchers have employed computer models of mosquito population growth and Dengue infection through time to answer questions about the optimal frequency of control interventions[18, 19] and about early detection of epidemics.[20,21] Studies that research what time of the year is most appropriate for control, our focus here, however, are rarer.

Direct study of control timing requires experimenting over large areas and relatively long time periods. We believe, however, that substantial information may be obtained indirectly, via the study of mosquito population dynamics. Sensitivity analysis is a tool, developed for the study of age or size-structured populations, by which one may ask how a small change in one of the population parameters, such as immature survival or adult fertility, impacts on a descriptor of the population state, such as size or growth rate.[22] Sensitivity analysis thus helps identify which parameters, when modified, produce the most cost-effective impact on a state variable of interest. Tran et al.,[23] Ellis et al.,[24] and Luz et al.,[19] for example, employed sensitivity analysis of mosquito population models to infer what were the life-stage-specific demographic rates to which different metrics of mosquito population state are most sensitive. In a different but related study, Emery and Gross[25] also employed sensitivity analysis, this time to infer what is the best time of the year for controlled burning of an invasive plant species. In our study, we apply sensitivity analysis, not to a structured model of the mosquito population, but to a site-occupancy model of mosquito infestation. Our model, informed by field observations from the Brazilian city of Porto Alegre, enables us to identify the time of the year when overall infestation is most sensitive to changes in the occupancy-dynamics parameters that explain the expansion and contraction of mosquito distribution in space. Effective control measures affect those occupancy-dynamics parameters, and, therefore, our sensitivity results identify times of the year that may be most appropriate for control.

MATHERIALS AND METHODS

Study Setting

Our study examines *A. aegypti* infestation in Porto Alegre, the largest city of Rio Grande do Sul, the southernmost state in Brazil (Figure 1). The city proper has approximately one and a half million habitants, whereas the metropolitan area has more than 4 million. The city's climate is subtropical humid, with hot summers, mild winters, and rainfall evenly distributed throughout the year. *A. aegypti* was first recorded in Porto Alegre in 2001 and it is now present in all the city's neighborhoods. Locally transmitted Dengue cases have been recorded since 2010, mostly in late summer and early fall. The largest outbreak happened in 2016, with 301 confirmed cases. Currently, municipal Dengue control relies on peridomestic insecticide spraying as well as on community-based actions to eliminate breeding sites. Spraying is only applied when local infection is happening, taking place in locations frequented by infected patients, with the objective of suppressing further infections.

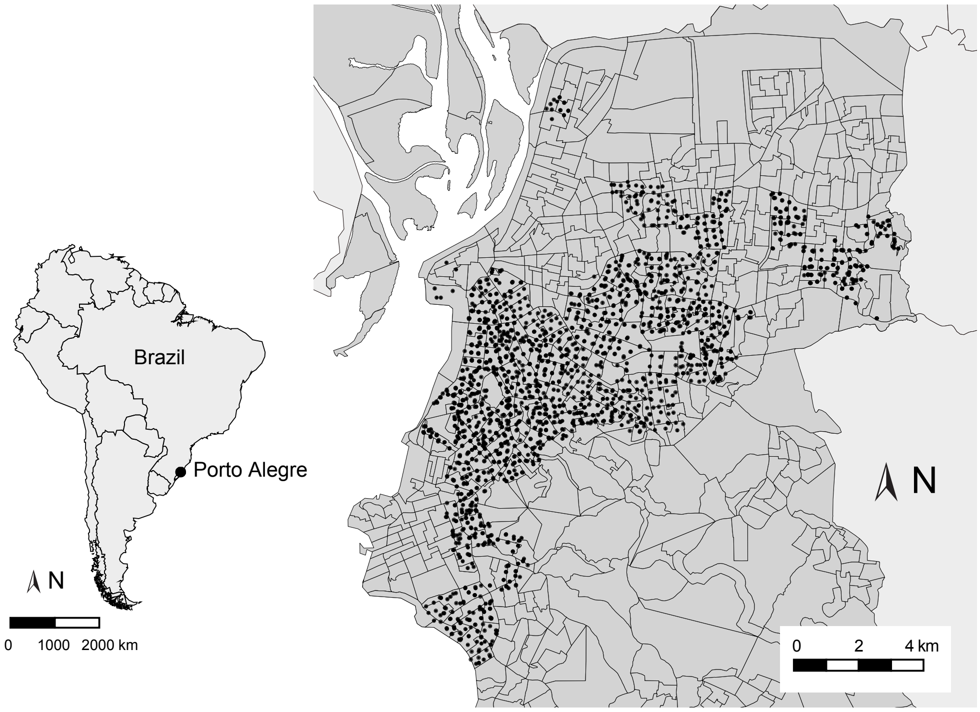

Figure 1. The city of Porto Alegre, with its location in South America (left) and the distribution of adult mosquito trapping sites throughout the city (right). Map lines show sampling unit boundaries. Black dots show all the sites sampled at least once throughout the 4 years of monitoring included in this study.

Data Collection

We analyzed data collected by the *Núcleo de Vigilância de Roedores e Vetores* (NVRV) of the Porto Alegre Municipal Department of Health, from September 23rd 2012, to August 14th 2016. Sampling spanned 204 weeks and consisted of weekly deployment of hundreds of adult mosquito traps throughout the city. The number of traps deployed in one week ranged from 481, in September 23rd 2012, to 893, in October 8th 2016, steadily increasing through time according to the availability of resources and the monitoring priorities of the NVRV. The choice of trapping locations followed the spatial distribution of confirmed Dengue cases and evidence of high *Aedes* spp. infestation. Traps were deployed outdoors either in public or private places and with a minimum distance of 250 meters from each other. There was some inevitable relocation of traps throughout the study period, mostly due to changes in accessibility to trapping sites that were beyond the control of the NVRV.

The NVRV uses a commercially available adult mosquito trap (Mosquitraps®, Ecovec, Belo Horizonte, Brazil), which consists of a 30-centimeter-high black plastic cylinder with a funnel-shaped opening on top. When deployed, traps were half filled with water treated with a slow-release chemical attractive that mimics the effects of a hay infusion (AtrAedes®, Ecovec, Belo Horizonte, Brazil). Female mosquitoes attracted by the odor enter the cylinder to lay eggs, get trapped by the funnel access, and eventually stick to an adhesive ribbon that lines the inner wall of the trap. Each NVRV agent is responsible for approximately 55 traps that she visits once a week, from Monday to Friday. On each visit to each trap, agents remove the adhesive ribbon and check for glued mosquitoes. If the ribbon has any mosquitoes that the agent identifies as being a female *A. aegypti*, the mosquito is sent to a laboratory to test for Dengue, Chikungunya, and Zika viruses.

For the purpose of our analysis, we outlined 756 sampling units (Figure 1) on a map of Porto Alegre land cover and use (the Porto Alegre Environmental Diagnostic map[26]) overlaid with a map of the Brazilian federal government human socio-economic census sectors.[27] While outlining units, we sought to homogenize socio-economic and land use variables within each unit. Although we also tried to keep unit area as constant as possible (mean ± SD of 28.9 ± 16.9 ha), the geography of land cover and use combined with limits of census sectors resulted in a range of areas spanning three orders of magnitude, from approximately 5 to 150 ha. Nonetheless, more than half of the units have between 20 and 32 ha in area. Our data set contains mosquito trapping data from 286 out of the 756 units in the city. Of these 286 units, there was an average of 2.5 ± 2.1

traps per site per week. Traps deployed in the same unit and week are treated as replicate samples of a closed system, so that if trap *k* detects *A. aegypti* on unit *j* and week i, any failure to detect mosquitoes in other traps from the same unit and week will be treated as a false negative result. We will refer to the deployment of one set of traps in one unit and week as a *trapping event*. The result from one trapping even is said to be *positive* if at least one of the traps captures one mosquito during that event.

Data Analysis

We modelled trapping data using Royle and Kéry's[28] Bayesian state-space implementation of the site-occupancy dynamics model developed by MacKenzie et al.[29] This model formally separates the biological process of unit infestation from the sampling process of mosquito trapping, with the latter conditioned on the former. The infestation state is represented by the partially observable variable $z_{i,t}$, which takes the value 1 when unit *i* is infested by *A. aegypti* at time *t*, and the value 0 otherwise. The trapping data is represented by the variable $y_{i,t,j}$, which takes the value 1 when trap *j* detects *A. aegypti* mosquitoes on unit *i* and week *t*, and the value 0 otherwise. We say that $y_{i,t,j}$ is conditioned on $z_{i,t}$ because there can be no positive trap results for $y_{i,t,j}$ when $z_{i,t} = 0$.

The dynamic component of the model describes changes in infestation through time as a first-order Markov process, where the value of $z_{i,t}$ depends on the value of $z_{i,t-1}$. At the outset, when *t* = 1, we model the infestation state $z_{i,1}$ as a Bernoulli trial with infestation probability $\psi_{t,1}$, estimated from the data:

$$z_{i,1} \sim \text{Bern}(\psi_{i,1}). \tag{1}$$

Subsequently, changes in infestation are given by the probabilities of local extinction, ε_t, and colonization, γ_t, also estimated from the data. The parameter ε_t represents the probability that a unit infested at time *t* will not be infested at time *t* + 1; conversely, γ_t represents the probability that a unit that is not infested at time *t* will be infested at time *t* + 1. Thus, the infestation state after the first week will be a Bernoulli trial with probability $\psi_{i,t+1}$ given by:

$$\psi_{i,t+1} = \left(1 - z_{i,t}\right) * \gamma_t - z_{i,t} * (1 - \varepsilon_t). \quad (2)$$

Thus, if a site is not infested at time *t*, $\psi_{i,t+1}$ equals γ_t; if it is infested, $\psi_{i,t+1}$ equals $1 - \varepsilon_t$, which can also be described as a probability of local persistence.

We also want to take into account, however, that γ_t and ε_t are not constant through time. In fact, they must vary cyclically throughout the year because the infestation follows a year-long cycle. To capture this periodic cycling in a mathematical form, we adapted the model to represent temporal change in γ_t and ε_t by the following trigonometric functions in logit space:

$$\text{logit}(\gamma_t) = \alpha_\gamma + \beta_\gamma \cos(2\pi\,(\tau_t - \tau 0_\gamma)), \quad (3)$$

$$\text{logit}(\varepsilon_t) = \alpha_\varepsilon + \beta_\varepsilon \cos(2\pi\,(\tau_t - \tau 0_\varepsilon)). \quad (4)$$

These functions measure time as a continuous variable τ, which varies between zero and one. Our dataset keeps track of time with an integer week counter; therefore, for a given week t, τ_t is the mean Julian day of the week divided by the total number of days in the year. The parameters α, β, and $\tau 0$, indexed by dynamic parameters γ or ε in equations 3 and 4, respectively, are estimated from the data. Parameter α gives the corresponding dynamic parameter mean value, β gives the amplitude of the cycle, and $\tau 0$ gives the time—in τ units—at which the dynamic parameter takes its maximum value.

The sampling component of our model is much simpler, since it treats the probability p of detecting *A. aegypti* mosquitoes at trap *j* of infested unit *i* on time *t* ($y_{i,t,j} = 1$) as being constant through time, across sites, and between traps of the same site. Formally, this consists of modeling the binary detection data $y_{i,j,t}$ as a Bernoulli trial with probability $z_{i,t} * p$:

$$y_{i,j,t} \sim \text{Bern}\left(z_{i,t} * p\right). \tag{5}$$

This equation captures the hierarchical nature of the model, as it conditions the possibility of a non-zero detection probability on the biological state of the system.

We fit our model to data in a Bayesian framework with uninformative priors, sampling from the posterior distribution of model parameters with a Markov Chain Monte Carlo (MCMC) algorithm.[30] The algorithm was implemented with the software JAGS,[31] accessed through R[32] with the library jagsUI.[33] We ran 3 chains with 15,000 iterations and a burn-in of 2,500 iterations. Model code can be found in Supplemental Material Appendix 1.

Part of our inference is based on metrics derived from the dynamic parameters of the site-occupancy model. We derived three infestation and two sensitivity metrics from the posterior samples given by the MCMC. The infestation metrics are also described on Royle and Kéry[28] as general occupancy metrics.

The *predicted equilibrium infestation* denoted $\psi_t^{(eq)}$, is the infestation probability that the system converges to if γ_t and ε_t remain constant for a sufficient time. We obtained $\psi_t^{(eq)}$ for each week of the study period, from the respective values of γ_t and ε_t,:

$$\psi_t^{(eq)} = \frac{\gamma_t}{\gamma_t + \varepsilon_t}. \tag{6}$$

A second infestation metric, *infestation probability*, represents the expected infestation rate on the theoretical infinite statistical population of units from which our sample was obtained. This metric is equal to ψ_1 when $t = 1$ and in all subsequent times is given by:

$$\psi_t = (1 - \psi_{t-1}) * \gamma_t + \psi_{t-1} * (1 - \varepsilon_t), \tag{7}$$

The third infestation metric is the *finite sample infestation*, which expresses the actual proportion of sample units infested at time *t*. We denoted this metric $\psi_t^{(fs)}$ and obtained it from a function of the latent variables:

$$\psi_t^{(fs)} = \frac{1}{M} \sum_{i=1}^{M} z_{i,t}, \tag{8}$$

with M representing the total number of sampling units, in this case 286.

In order to evaluate the extent to which changes in the dynamic parameters—eventually provoked by control measures—affect the equilibrium infestation probability, we also obtained two sensitivity metrics, $s_{\gamma,t}$ and $s_{\varepsilon,t}$, which measure the sensitivity of $\psi_t^{(eq)}$ to infinitesimal changes in, respectively, γ_t and ε_t. We derived sensitivities as proposed by Martin et al.,[34] using the equations:

$$s_{\gamma,t} = \frac{\varepsilon_t}{(\varepsilon_t+\gamma_t)^2}, \text{ and} \tag{9}$$

$$s_{\varepsilon,t} = \frac{\gamma_t}{(\gamma_t+\varepsilon_t)^2}, \tag{10}$$

which give de derivatives of $\psi_t^{(eq)}$ respectively on γ_t and ε_t

RESULTS

We gathered data from 150,453 trapping events, 33,499 (~22%) of which returned positive results. The greatest proportion of positive results on any given week was 0.627, in week 131, the last week of March 2015. Throughout the whole 204-week study period, there were only 4 weeks with no positive traps at all. This happened in weeks 47, 49, 50—late August and early September 2013—and in week 201, at the end of July, 2016. Observed infestation, given by the ratio of sites with positive results to all sites sampled in one week, ranged from 0.854, in week 131, to 0, in weeks 47, 49, 50 and 201. The mean observed infestation was 0.434.

Detection probability, or the probability of obtaining a positive result at a site that is infested, was estimated as 0.37±0.002. If only one trap were set per location, the observed infestation would be less than half its true value. With 3 traps per site, which is close to the average number of traps per sampled site in this study, the probability of obtaining at least one positive result at any given time is approximately 0.75.

The annual oscillation in mosquito infestation is evident from the temporal variation of $\psi_t^{(eq)}$ (Figure 2). Predicted equilibrium infestation ranges from a minimum of 0.10±0.003 in late July (July 25) to a maximum of 0.97±0.002 in early February (February 5). Overall, the $\psi_t^{(eq)}$ estimates predict that the Porto Alegre *A. aegypti* population spends more time per year increasing (from August to late January) than decreasing, from early February to the end of July. The annual decline in predicted equilibrium infestation in the Fall is slightly steeper than its increase in Spring.

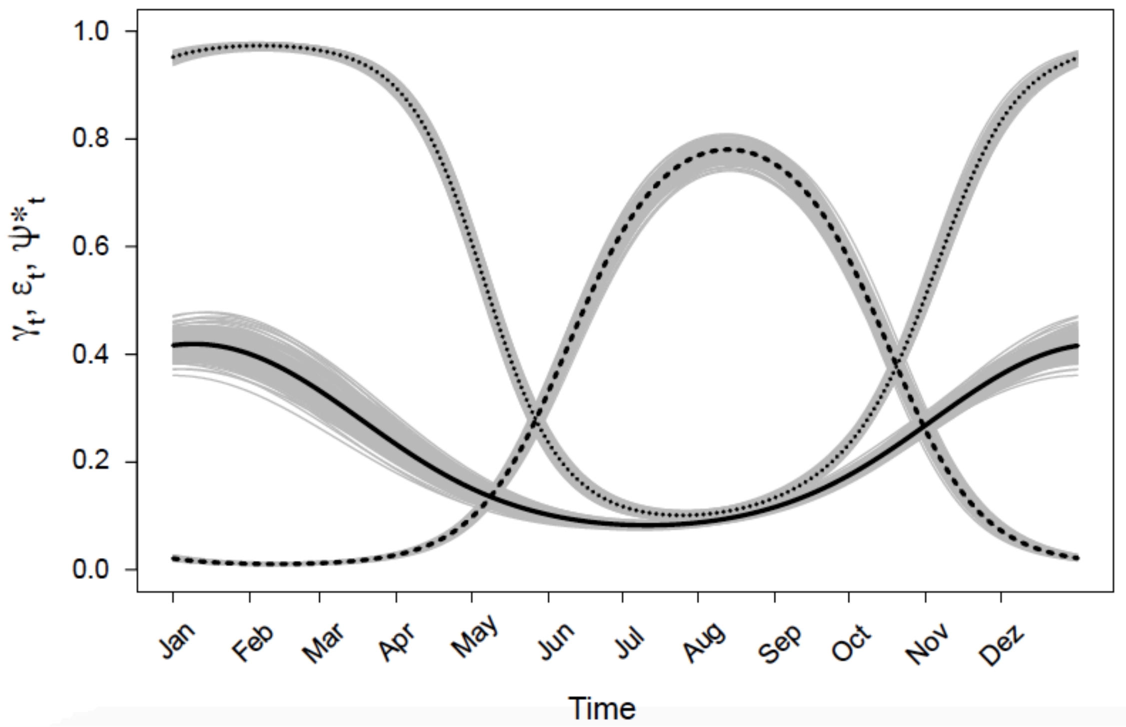

Figure 2. Variation of colonization probability (solid line, γ_t), local extinction probability (dashed line, ε_t) and equilibrium occupancy (dotted line, $\psi_t^{(eq)}$) throughout the year. Black lines (dashes or dots) show mean predicted values for each day, gray shading around the black lines represents uncertainty about the predicted values. Each shade includes 250 predictions of the respective variation, each prediction resulting from one sample of underlying (α, β, and $t0$) parameters from their respective posterior distributions.

Variability in $\psi_t^{(eq)}$ reflects variability in local extinction (ε_t) and colonization (γ_t) rates. On average, ε_t peaks just after the middle of Winter, at 0.78±0.012 on August 12, a few weeks after the minimum value of $\psi_t^{(eq)}$. The minimum value of ε_t is 0.01±0.001, corresponding to February 11, just after the peak predicted equilibrium infestation. The colonization rate also oscillates, albeit with lower amplitude, from 0.08±0.004 on July 11 to 0.42±0.020 on January 9, its variation nearly coinciding with variation in $\psi_t^{(eq)}$.

Seen throughout the whole study period, $\psi_t^{(eq)}$ closely follows ψ_t the infestation probability (Figure 3). Observed infestation is often lower than both $\psi_t^{(eq)}$ and ψ_t. In the abnormally warm winter of 2015, observed infestation was exceptionally high, and higher than $\psi_t^{(eq)}$ or ψ_t, which do not express variation between years. The infestation metric that best captures inter-annual variation is the finite sample infestation, which oscillated from 0.98±0.007 in week 127 (last week of February 2015) to 0.03±0.010 in week 201(one of the weeks without mosquito detection).

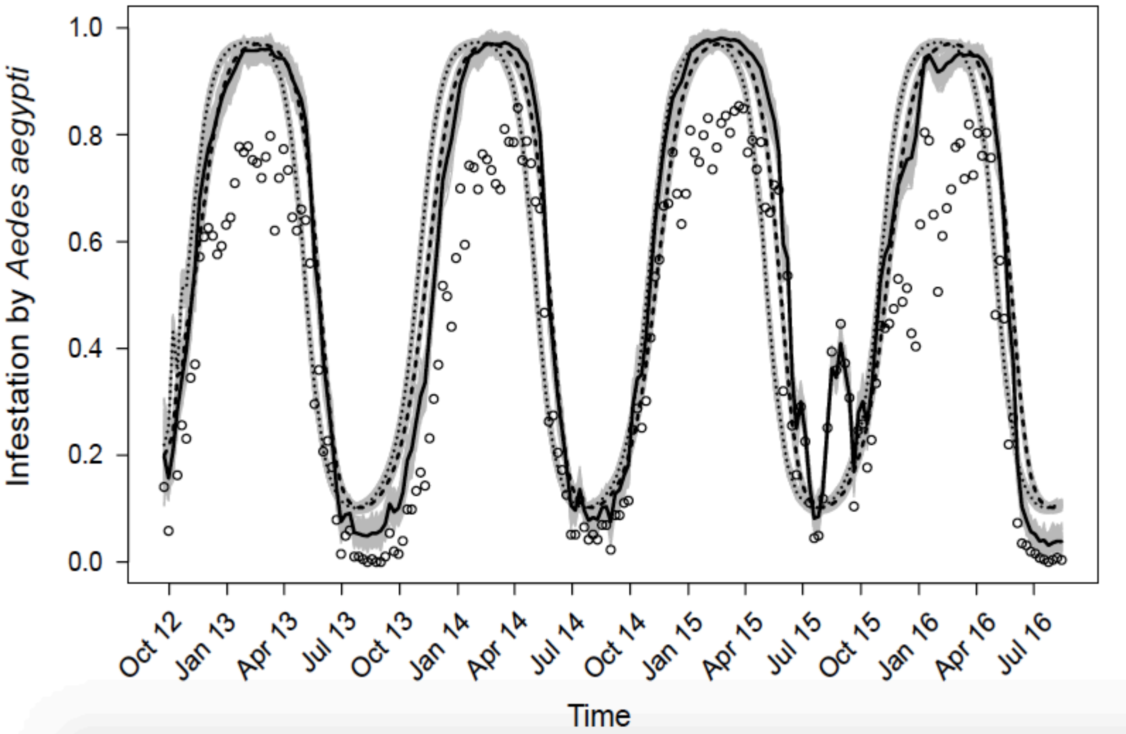

Figure 3. Different metrics of infestation by *A. aegypti* throughout the sampling period. Empty circles show observed infestation, the proportion of sampled sites which had at least one *A. aegypti* capture in the corresponding week. The three black lines show the mean values for three estimates of infestation probability: finite sample infestation ($\psi_t^{(fs)}$; solid line), population infestation (ψ_t; dashed line), and equilibrium infestation predicted under current dynamic parameter (ε_t, γ_t) estimates ($\psi_t^{(eq)}$; dotted line). Gray shading around the black lines represents 250 infestation predictions for each black line, each prediction based on one random sample of parameters (α, β, and $t0$) from the posterior.

The variation of sensitivity throughout the year has a greater amplitude for ε_t ($s_{\varepsilon,t}$) than for γ_t ($s_{\gamma,t}$; Figure 4) reflecting the greater oscillation in the values of ε_t. During the austral summer and fall months, when ε_t is smaller than γ_t, sensitivity to changes in extinction probability ($s_{\varepsilon,t}$) tends to be greater than sensitivity to changes in colonization ($s_{\gamma,t}$); the reverse being true for the winter and spring months, when γ_t is smaller than ε_t. The months of March to July comprise the period of highest sensitivity for both dynamic parameters.

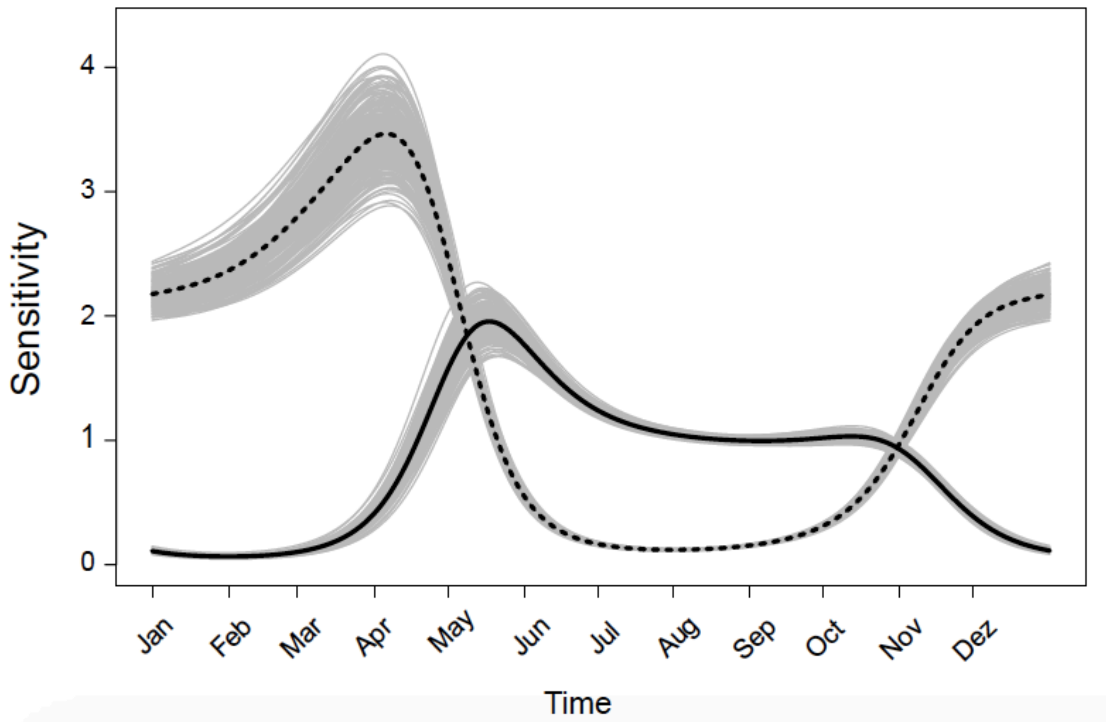

Figure 4. Sensitivity of equilibrium occupancy to changes in probability of colonization (solid line) and probability of extinction (dashed line), as it varies throughout the year. Gray shading around the black lines represents 250 predictions of the same variation, based on random samples of underlying parameters (α, β, and $t0$) from their posterior distributions.

DISCUSSION

Our analysis of site-occupancy by *A. aegypti* in the city of Porto Alegre uses adult mosquito trapping data to fit a model of neighborhood infestation dynamics along a typical year. The resulting trigonometric function shows infestation fluctuating from almost full occupancy throughout the city on summer months to nearly 10% of neighborhood occupancy during the peak of winter, so that adult mosquitoes are never completely absent. Colonization and local extinction probabilities fluctuate out of phase throughout the year, with peaks respectively in late summer and late winter, separated by half a year. The period when equilibrium occupancy is most sensitive to variations in colonization and extinction probabilities is the Fall, suggesting that mosquito control should be most effective during the months of April, May and June.

The modeling approach at the core of this study stands on two choices that merit clarification prior to further discussion of the results. First, our model follows a site-occupancy approach. That is, we focus not on the number of individual mosquitos at a given site, but at the occupancy state of each site. Second, we take a phenomenological, not a mechanistic path towards prediction of the annual cycle of mosquito infestation. Our interest on the occupied versus non-occupied state of sites is akin to the well-established research approach known as metapopulation biology and employs mathematical abstractions initially developed for the study of agricultural pests.[35] The metapopulation approach aims at understanding population dynamics over many sites, where the fate of an aggregate of sites depends more on the movement of individuals between sites than on demography within each site. Site-occupancy dynamics is thus captured by the twin metrics of local extinction and colonization probability, which measure the probability of transition between site states. From an applied perspective, mosquito control measures aim to maximize local extinction and/or minimize colonization, in order to reduce mosquito population below a level of transmission risk. Within this analytical framework, one can evaluate the timing of control measures through the sensitivity analysis proposed by Martin et al.,[34] which measures the extent to which a given change in transition probabilities affects the equilibrium site-occupancy probability. We seek the analytical advantages of the site-occupancy approach but note that a positive relationship between abundance and occupancy is a common feature of many populations[36] that has already been documented in *A.*

aegypti.[37,38]

Our second choice, of building a phenomenological model of occupancy dynamics, was guided by an interest in generic, prediction-based management recommendations, applicable to any future year and not just to the peculiar environmental conditions of a given observation period. If our goal were to test hypotheses about the mechanisms underpinning population dynamics, it would be appropriate to build a mechanistic model. Such model should include as independent variables the environmental factors that hypothetically condition population change. In the current analysis, however, we wanted to predict mosquito infestation and sensitivity to control measures at any time of a typical year, without the need for local environmental information. To achieve this goal, we found it reasonable to model the temporal variation of ε_t and γ_t as a mathematical abstraction determined only by time, under an oscillatory behavior of period equal to one year, or one full cycle of four seasons. The choice of a phenomenological approach obviously comes with a price. For example, the exceptionally warm winter of 2015 produced a peak in infestation that is not captured by our oscillatory model. Nonetheless, we find the agreement between observations and oscillatory predictions throughout the rest of the study period encouraging enough to support our approach in the context of our current goals.

Phenomenological or mechanistic, any hierarchical model of site occupancy offers the advantage of accounting for imperfect detection. In our case, the model estimates the probability p that a trap detects mosquito presence at a site that is actually infested. Our estimate of $p \sim 0.33$ implies that in approximately two out of three instances one trap will fail to detect mosquito presence at an infested site. This provides substantial motivation for using more than one trap per site and strengthens the notion that assuming perfect detection ($p = 1$) leads to negatively biased infestation estimates.

While accounting for imperfect detection, our results identify four distinct periods of a yearly infestation cycle that roughly correspond to the four seasons. The austral Summer months of January, February and March comprise the longest stretch of high and steady infestation, with mosquitoes present throughout nearly the entire city. The Fall season, corresponding to April-June, shows a sustained decline in infestation until a new period of relatively steady but low (ψ ~0.1) mosquito presence is attained in the Winter months. Finally, during the months of October-December, spring weather accompanies the recovery of infestation throughout the city, until infestation reaches again the high levels typical of the Summer months and the cycle starts over again. Although the oscillation of mosquito presence does not come as a surprise to anyone familiar with Porto Alegre, our results offer a timing of the cycle and a quantitative assessment of its amplitude, which is relevant and new. With weekly estimates of ψ ranging from ~0.1 to ~1, Porto Alegre can be placed in Scenario 2 of Eisen et al.'s[3] classification of cities according to year-round activity of *A. aegypti*. Scenario 2 corresponds to locations with "year-around activity but potential for high abundance of the active stages only during the most favorable part of the year".[3] Cities classified under Scenario 2 have subtropical climate with an unfavorable cold season, or tropical climate with an unfavorable dry season. Similarities in climate likely entail similarities in mosquito population dynamics, such as a clear annual oscillation in infestation without complete disappearance of adult mosquitoes during the most unfavorable months. The permanence of infestation throughout the year motivates epidemics prevention strategies based on constant monitoring of disease cases and application of mosquito control measures only to suppress further infections. Such strategies have been applied in Porto Alegre, Brazil[39], and in other cities classified as Scenario 2 such as Cairns, in Australia.[40]

Cyclical variation in infestation is the outcome of cyclical variation in local extinction and colonization rates. The relationship between dynamic parameters and occupancy is clearly outlined in our model, but the underlying relationship between mosquito demographic parameters of individual mortality and transition between development stages is more difficult to grasp. It is reasonable to expect that local extinction probability will have a positive relationship with adult mortality and a negative relationship with adult emergence from the pupal stage. Likewise, colonization should be related to the same two demographic parameters, albeit with different signs: increased adult mortality should decrease colonization rates, while increased emergence should have the opposite effect. Changes in one demographic rate, however, such as adult mortality or pupal emergence, may affect both the local extinction and the colonization rates. Nonetheless, we can assert from our results that a) the variation of local extinction throughout the year shows greater amplitude than the variation of the colonization rate; and b) that the two occupancy-dynamics parameters vary almost exactly out of phase, with a lag of approximately one month between one parameter’s maximum and the other’s minimum values. Why this should be so is still open to investigation, pending a more detailed understanding of the biological mechanisms driving each of the dynamic rates.

Even without precise knowledge of the biological mechanisms that cause temporal variation in colonization and local extinction, we can use this variation to draw inference about the most appropriate timing for control measures. Such measures are often applied in response to locally high values of vector infestation or disease transmission. The appropriateness of a responsive approach, however, should not preclude the preemptive application of control measures. Clearly, though, the effectiveness of preemptive control depends on timing. We suggest that sensitivity metrics offer useful timing criteria, because they identify when a unit change in local extinction or colonization has the greatest effect on infestation, as measured by the equilibrium occupancy estimate. This is tantamount to identifying the period at which the mosquito population is most vulnerable to control. Interestingly, the peaks of sensitivity to variation in both local extinction and colonization rates fell within the same period from April 13 to May 25, which corresponds roughly to the Austral Fall. So, even though we cannot establish a straightforward connection between alternative control measures and the two occupancy dynamic rates, we identify a relatively narrow period during which any form of control that affects colonization or local extinction probability should reach its maximum effect.

One note of caution, regarding the timing criterion, is that it rests on the validity of equilibrium occupancy as a metric of infestation. Equilibrium occupancy is the occupancy that would be attained at equilibrium if the current dynamic parameters remained constant for sufficient time. Considering the temporal variation in dynamic parameters that is embedded in our model, one might find reason to doubt the validity of the metric, especially if there were evidence that the Spring recovery in infestation is the result of immigration from outside Porto Alegre. Nevertheless, we do not know of any such evidence and we found a remarkable proximity in the estimated values of equilibrium and population infestation in Figure 3. It is also reasonable to think that control measures in the fall will reduce the winter egg stock and thus limit infestation through the whole next year. Coincidentally or not, a study of spatio-temporal patterns of dengue epidemic events in Argentina found a positive relationship between average Fall temperature and the number of dengue cases reported in the subsequent year.[41] One way to test the relevance of focusing control measure in the fall would be to perform a controlled experiment where urban areas that are continuously monitored for infestation receive a treatment of intensive mosquito population control during the Fall months. We believe that the results presented in our study provide sufficient motivation for such an experiment.

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Disclosure

The authors report no conflict of interest.

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Considerações finais

Nesta dissertação, produzi resultados que são interessantes por si só, mas que também servem para ressaltar os pontos positivos da abordagem de modelagem hierárquica de parâmetros populacionais para o problema do *A. aegypti*. Descrevi a dinâmica intra-anual da população de *A. aegypti* em Porto Alegre apresentando resultados úteis para os gestores se prepararem com antecedência para os períodos de maior infestação. Além disso, ao aplicar modelos parecidos em dezenas de outras cidades brasileiras em que o M.I. Aedes está presente, será possível identificar semelhanças entre elas. Com base nessas semelhanças, o Ministério da Saúde pode orientar estratégias de controle comuns para cidades com realidades entomológicas parecidas.

Com base na análise de sensitividade, propus a hipótese de que o controle do mosquito teria mais efeito a nível municipal se aplicado no outono. Um experimento pode ser planejado para testar esta hipótese, em que um ano com controle no outono é comparado a um sem controle, quanto ao nível de infestação. Se for comprovada, podemos abrir caminho para uma estratégia de controle em cidades como Porto Alegre que impeça preventivamente o mosquito de alcançar abundância que propicie epidemia.

Apesar dos avanços, as minhas decisões analíticas tiveram fraquezas. Algumas delas são consequências de tentar analisar uma base de dados já existente, ao invés de planejar a amostragem. Assim tive que fazer premissas mais fracas que o ideal, como, por exemplo, da homogeneidade entre áreas amostrais. A abordagem de ocupação de sítios também revelou uma fraqueza: com praticamente toda cidade infestada no verão, não seria possível identificar áreas de risco somente com essa abordagem. Seria necessário estimar a abundância local do mosquito nos diferentes sítios. Espero que com a popularização da modelagem hierárquica de parâmetros populacionais em estudos sobre o *A. aegypti* e amostragens planejadas especificamente para tal, estas e outras dificuldades possam ser superadas coletivamente pela Ciência visando construir estratégias mais eficientes em prevenir os danos que as arboviroses causam à vida das pessoas.