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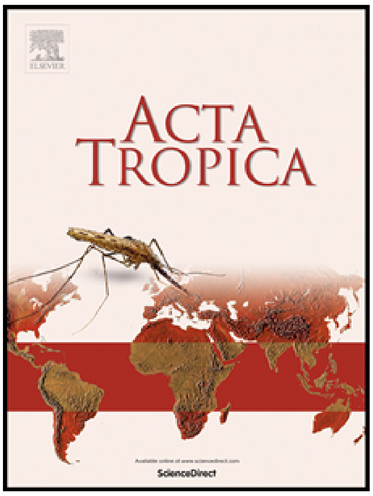

Understanding the role of temporal variation of environmental variables in predicting Aedes aegypti oviposition activity in a temperate region of Argentina

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Highlights

- Environmental variables are key factors in the modeling of *Aedes aegypti* oviposition
- Vegetation, vapor pressure, rainfall and photoperiod are predominant variables
- Minimum temperature is an important factor that limit the vector activity in Córdoba
- Predictive models are useful tools in temperate cities that help vector surveillance

Understanding the role of temporal variation of environmental variables in predicting *Aedes aegypti* oviposition activity in a temperate region of Argentina

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Abstract

Environmental variables related to vegetation and weather are some of the most influential factors that impacting *Aedes* (*Stegomya*) *aegypti*, a mosquito vector of dengue, chikungunya and Zika viruses. In this paper, we aim to develop temporal predictive models for *Ae. aegypti* oviposition activity utilizing vegetation and meteorological variables as predictors in Córdoba city (Argentina). Eggs were collected using ovitraps placed throughout the city from 2009 to 2012 that were replaced weekly. Temporal generalized linear mixed models were developed with negative binomial distributions of errors that model average number of eggs collected weekly as a function of vegetation and meteorological variables with time lags. The best model included a vegetation index, vapor pressure of water, precipitation and photoperiod. With each unit of increment in vegetation index per week the average number of eggs increased by 1.71 in the third week. Furthermore, each millimeter increase of accumulated rain during 4 weeks was associated with a decrease of 0.668 in the average number of eggs found in the following week. This negative effect of precipitation could occur during abundant rainfalls that fill containers completely, thereby depriving females of oviposition sites and leading them to search for other suitable breeding sites. Furthermore, the average number of eggs increased with the photoperiod at low values of mean vapor pressure; however the average number of eggs decreased at high values of mean vapor pressure, and the positive relationship between the response variable and mean vapor pressure was stronger at low values of photoperiod. Additionally, minimum temperature was associated positively with oviposition activity and that low minimum temperatures could be a limiting factor in *Ae. aegypti* oviposition activity. Our results emphasize the important role that climatic variables such as temperature, precipitation, and vapor pressure play in *Ae. aegypti* oviposition activity and how these variables along with vegetation indices can be used to inform predictive temporal models of *Ae. aegypti* population dynamics that can be used for informing mosquito population control and arbovirus mitigation strategies.

Keywords: *Aedes aegypti*; Córdoba city; Temporal predictive models; Environmental variables.

1. Introduction

Aedes aegypti, a vector of dengue, chikungunya and Zika viruses, is a species distributed widely throughout the world. It is a successful synanthropic mosquito, taking advantage of different breeding sites similar to those used in its original habitat (Stein et al.

2016). Whether this species and its pathogens become successfully established depends upon the characteristics of the area in which it is introduced, but it has been introduced and become established in regions that have a variety of characteristics (Carbajo et al. 2012). *Aedes aegypti* is distributed widely through tropical and subtropical regions; however, the distribution range of both the vector and its associated pathogens have extended to many temperate areas (Khormi and Kumar 2014, López-Latorre and Neira 2016).

Much effort has been invested in better characterizing environments in which mosquito populations could become established. For more than 20 years, data obtained from satellites have been used as an aid to characterize these environments (Beck et al. 1994, Estallo 2016). For urban mosquitoes such as *Ae. aegypti*, the Land Surface Temperature (LST) and the Normalized Difference Vegetation Index (NDVI) are the most frequently used satellite variables for spatial and temporal studies (Estallo et al. 2012, 2016, 2018, German et al. 2018, Scavuzzo et al. 2018, Tsai et al. 2018, Ordoñez-Sierra et al. 2020). Based on the way vegetation indices are calculated and its interpretation, they are used as indirect indicators of seasonal climatic variability (Estallo, 2016) that influences the vegetation dynamics (Liu et al. 2015). Therefore, many times these indices have been used to predict the seasonal activity of species of sanitary importance such as *Ae. aegypti* since there is a strong positive association between them (Estallo et al. 2016).

In addition, meteorological variables are effective predictors of *Ae. aegypti* abundance (Estallo et al. 2015, da Cruz Ferreira et al. 2017). Temperature is one of the variables often used in predictive models of *Ae. aegypti* abundance due to its influence on key life history features of these mosquitoes such including adult longevity, female fecundity (Marinho et al. 2016), adult size, immature development, and immature survival rates (Tun-Lin et al. 2000, Tsai et al. 2018), as well as its important relationship with epidemiologically important measures such as vectorial capacity (Liu-Helmersson et al. 2014). In fact, minimum temperature is directly related to vector abundance (Estallo et al. 2011, da Cruz Ferreira et al. 2017), and affects measures of flight performance such as distance flown, duration, and speed (Rowley and Graham 1968). Precipitation is another variable frequently used which is generally positively associated with *Ae. aegypti* abundance (Barrera et al. 2011). This is because rainfall fills containers and this increases the number of breeding sites which directly increases the abundance of the vector (Eisen et al. 2014). Furthermore, there is evidence that these meteorological variables also influence the incidence of diseases transmitted by *Ae. aegypti,* such as dengue (Hii et al. 2012, Xu et al. 2017).Despite the importance of these vegetation indices and meteorological variables, it should be noted that their relationships with vector activity and dengue cases can vary with the study area and the sampling scale; possibly due to the influence of other local variables (Carbajo et al. 2012, Choi et al. 2016). For this reason, it is important to consider spatial and temporal variation in vector activity in order to develop the best management strategies. For *Ae. aegypti*, surveillance using ovitraps is one of the most effective and lowest cost methods to determine distribution and the seasonal fluctuation of the populations (Vargas 2002). Predictive models based on vegetation and meteorological variables that characterize some aspects of the environment and environmental influences on vector dynamics are useful tools for the surveillance and control of these mosquitoes; they also help to assess the risk of disease outbreak.

Based on the results found in previous studies, we expect that temperature and precipitation, as well as vegetation, would affect *Ae. aegypti* oviposition activity in Córdoba city more than other variables like humidity, vapor pressure of water, and photoperiod. Although these latter three variables have been studied less thoroughly, there is evidence that they can have an important effect on the oviposition activity of the vector (Dominguez et al. 2000, Costa et al. 2010, Estallo et al. 2015). We hypothesize that when temperature and precipitation increase, so would the number of eggs laid in subsequent weeks. Furthermore, we hypothesize that when the vegetation indices increases, the number of eggs would rise because temperature and precipitation regulate, to some extent, vegetation development, and increases in vegetation are associated with warmer temperatures and mainly increased precipitation (Liu et al. 2015). Therefore, we aim to develop temporal predictive models for *Ae. aegypti* oviposition activity that investigate as predictors vegetation and meteorological variables in Córdoba city, a temperate area of Argentina.

2. Material and Methods

2.1. Ethics statement

Ovitrap sampling was carried out under the *Ae. aegypti* surveillance program of the Ministerio de Salud de la Provincia de Córdoba therefore no written informed consent was required. The residents of the dwellings where ovitraps were placed provided oral informed consent.

2.2. Study area

The study took place in Córdoba city (31° 24' S, 64° 11' W) of Córdoba province, Argentina, which is in a temperate region (Fig 1). The climate is characterized by a cold and dry period from May to September and a warm and rainy period from October to April. According to the records from October 2010 to April 2017, the mean annual rainfall is 800 mm; during the dry and cold winter, the maximum and minimum average temperatures are 20°C and 8°C, respectively, and during the warm and rainy summer , the maximum and minimum average temperatures are 29°C and 16°C, respectively (Servicio Meteorológico Nacional 2018).

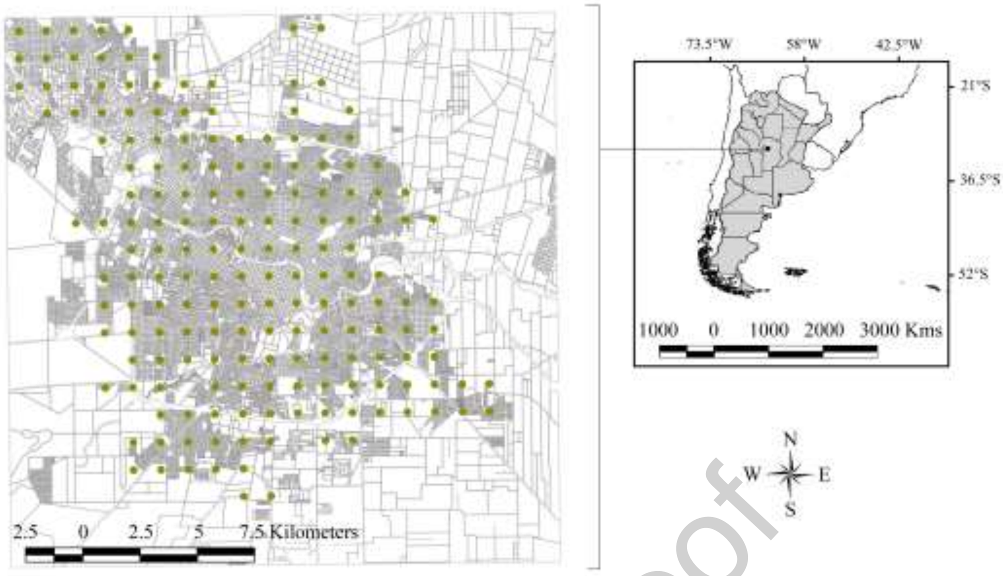

Fig 1. Study area where the samplings were carried out. The points mark the sites where the ovitraps were placed in Córdoba city, from 2009 to 2012. The inset figure shows the location of Córdoba city within the province of Córdoba in Argentina.

2.3. Ovitrap sampling

In Córdoba city there is no *Ae. aegypti* activity during cold months (Dominguez et al. 2000, Estallo et al. 2020). *Aedes aegypti* oviposition activity fluctuation was studied during three vector activity seasons, from November-December to May (2009-2010: Season 1, 2010-2011: Season 2, 2011-2012: Season 3), and the fluctuation was assessed weekly by ovitrap sampling. The study was carried out in 177 dwellings, distributed uniformly throughout Córdoba city (Fig 1). An ovitrap was placed outside each dwelling in a shaded area, protected from the rain and located at ground level. Ovitraps consisted of 350 ml transparent plastic jars (8 cm in diameter and 13 cm high), with a cylinder of brown heavy (120 g) rough paper inside that covered the entire interior wall. This paper, where the *Ae.*

aegypti females laid eggs, allowed us to easily count the eggs. Ovitraps were filled with 250 ml of grass infusion when settled. This infusion consisted of dry grass macerated in water for one week, which works as an attractant to gravid *Ae. aegypti* females (Reiter and Nathan 2001). Ovitraps were replaced weekly. At the laboratory, eggs within each ovitrap were counted. Sampling was carried out by the Department of Epidemiology of the Ministerio de Salud de la Provinca de Córdoba in cooperation with the mosquito team of the Instituto de Investigaciones Biológicas y Tecnológicas, IIBYT (CONICET-Universidad Nacional de Córdoba).

2.4. Vegetation and meteorological variables

Vegetation indices from MODIS products were used as vegetation variables. NDVI (MOD13Q1.006), EVI (MOD13Q1.006) and LAI (MOD15A2H.006) were retrieved from the online Application for Extracting and Exploring Analysis Ready Samples (AppEEARS), courtesy of the NASA EOSDIS Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota (https://lpdaacsvc.cr.usgs.gov/appeears/). Vegetation indices are used in the detection of green vegetation since they inform about the growth, vigor, and dynamics from terrestrial vegetation, which facilitates the estimation of the vegetation biomass in a determined area (Xue and Su 2017). In fact, vegetation could be considered an indirect estimator of environmental conditions such as humidity and precipitation since these regulate vegetation development (Estallo et al. 2012, 2016, Liu et al. 2015). In Table

1, the selected vegetation variables with their characteristics are shown (https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table).

Table 1. Vegetation variables obtained from MODIS products.

Variable	**Products**	**Spatial resolution**	**Temporal resolution**	**Description**
NDVI (Normalized Difference Vegetation Index)	MOD13Q1.006	250 meters	16 days	Quantifies the concentrations of green leaf vegetation. It is Chlorophyll sensitive and can identify drought and water stress (Gao et al. 2000).
EVI (Enhanced Vegetation Index)	MOD13Q1.006	250 meters	16 days	Responsive to canopy structural variations (leaf area index, canopy type, plant physiognomy, and canopy architecture) (Gao et al. 2000).
LAI (Leaf Area Index)	MOD15A2H.006	500 meters	8 days	Defined as the one-sided green leaf area per unit ground area in broadleaf canopies and as one-half the total needle surface area per unit ground area in coniferous canopies.

MODIS products were received as a single product for the whole of Córdoba city as a result of the merge of several products that covered the city. Each one of these products included data from September 6, 2009 to May 26, 2012. There were a few gaps in the data, because of differences in the frequency of the satellite data collection (16 days or 8 days depending on the product) and some variables were not measured at all time points. When gaps occurred, linear interpolation was used to estimate the variables at a weekly time scale in order to coincide with *Ae. aegypti* eggs weekly count data in subsequent analyses. From the products, we used the daily mean values of metrics of interest in our analyses.

Servicio Meteorológico Nacional (SMN) provided daily and hourly measurements for the sampling period, from the two weather stations placed for Córdoba city by the National Institution. Weekly meteorological data (maximum/minimum temperature, temperature range, accumulated rainfall, mean and minimum relative humidity, humidity range and mean vapor pressure of water) were calculated and used in data analysis. In addition, photoperiod was added as a variable, which has an effect on lifespan and blood feeding activity and affects survival (Costanzo et al. 2015). Considering the biological characteristics of *Ae. aegypti*, time lags were applied to the explanatory variables (Estallo et al. 2015, 2016), to consider delayed effects of these variables on *Ae. aegypti* response variables.

2.5. Data analysis

In our analysis, the response variable used was the weekly average number of *Ae. aegypti* eggs. A mean number of eggs counted per week was obtained from the 177 ovitraps. It is important to clarify that the weekly average was calculated only with active ovitraps; non-active traps, absent, and destroyed traps were excluded (Carbajo et al. 2006).

From the vegetation and meteorological variables we calculated one value for each variable for the city across a week to perform the analysis, as was mentioned in the previously. Correlations among environmental vegetation and meteorological variables and the response variable were investigated at different time lags, using the first and the second sampling season. We consider only the first two seasons here in order to train the model for making predictions in the third season. Time lags between one and seven weeks were used, taking into account that the approximate duration of a complete life cycle of *Ae. aegypti* lasts from 2 to 6 weeks in temperate regions (Christophers 1960, Dominguez et al. 2000). Time lags were calculated in two different ways for all explanatory variables. First, we considered values of the variables in a given week (**t-n**) to investigate how they correlated with the response variable in subsequent weeks (where **t** is a specific week in which ovitrap data is collected, **n** is the number of the weeks before **t**; **n** acquires values ranging from 1 to 7). For example, values of explanatory variables in **t-1** are values recorded in the week immediately prior to the week in which the eggs were collected, while values in **t-2** were recorded in the week immediately prior to the week **t-1**, and so on. Alternatively, we consider values of the explanatory variables in a time interval (**t-n, t-1**) to investigate their correlation with the response variable at time **t**. The interval can vary from 1 to 7 weeks. Therefore, an interval of **(t-2, t-1)** means that the values of the variables are taken from the interval that goes from 2 weeks before data was collected to the week before the collection of eggs, obtaining 1 value of the explanatory variable corresponding to the 14 days prior to the week in which the eggs are recorded. We calculated lags this last way in order to further consider variations in the values of the variables across an interval of time up to its influence on oviposition activity; unlike the first way that only contemplates data from one week that is reflected in the response variable weeks later.

A 168 potential explanatory variables were considered in our analysis; however, the number of variables was reduced by selecting those that best correlated with the response variable based on the best time lags from each vegetation and meteorological variable. The definition of the selected explanatory variables is shown below.

- **Vegetation indexes NDVI/ EVI/ LAI** (**NDVI(t–n)/ EVI(t–n)/ LAI(t–n)**): The mean vegetation index corresponding to the week number **n** before the week **t** in which the eggs were collected.
- **Maximum/ minimum temperature** (**TM(t–n,t–1)/ Tm(t–n,t–1)**): The maximum and minimum temperature reached during the **n** weeks immediately previous to the week **t** in which the eggs were collected.
- **Temperature range** (**Tr(t–n,t–1)**): The thermal amplitude from the **n** weeks immediately previous to the week **t** in which the eggs were collected.
- **Accumulated rainfall** (**RAIN(t–n,t–1)**): The accumulated rainfall in **n** weeks immediately previous to the week **t** in which the eggs were collected.
- **Average/ minimum relative humidity** (**RHa(t–n,t–1)/ RHm(t–n,t–1)**): The mean and minimum relative humidity reached during the **n** weeks immediately previous to the week **t** in which the eggs were collected.
- **Relative humidity range** (**RHr(t–n,t–1)**): The amplitude of relative humidity from the **n** weeks immediately previous to the week **t** in which the eggs were collected.
- **Mean vapor pressure of water** (**VP(t–n,t–1)**): The mean vapor pressure obtained during the **n** weeks immediately previous to the week **t** in which the eggs were collected.
- **Photoperiod** (**Ph(t–n,t–1)**): The accumulated light hours in **n** weeks immediately previous to the week **t** in which the eggs were collected.

Spearman's correlation coefficient was used to determine which time lags of each explanatory variable were best correlated with the response variable. In addition, correlation analyses were performed among explanatory variables to avoid multicollinearity in the models. Explanatory variables that had high correlation with others (Spearman's correlation coefficients greater than 0.7) were not incorporated into the same model. The average number of eggs per week (**O(t)**) was modeled as a function of the selected environmental variables using Generalized Linear Mixed-Effects Models (GLMM). The models were built based on the first two sampling seasons (December 2009-May 2010 and November 2010-May 2011). Months (**M**) differentiated by seasons were included as a random effect to incorporate temporal dependence. This means that we used months (**M**) as a factor, from the seasons 1 and 2, including 13 levels and at least 3 observations inside each level. Initially, decision tree and univariate models were performed to choose the most important explanatory variables and to start to develop the models, as well as identifying possible interactions between explanatory variables. Five specific models were established which were performed in Statistical software *R* v.3.6.2 (R Studio 2019), assuming a negative binomial distribution of errors with log link function. The models were built through the manual forward stepwise procedure. In each step significance of variables was evaluated and, when there were not significant variables to add, interaction among the significant variables from the model were added to improve model performance (Carbajo and Pardiñas 2007). The multicollinearity among variables was evaluated in the final models through the Variance Inflation Factors (VIF), considering a threshold value of 5 (Montgomery and Peck 1992). In addition, overdispersion, the normality of the residuals distribution, and temporal autocorrelation were checked. Models were ranked following the Akaike's Information Criterion (AIC) and the model with the lowest AIC was selected as the best model (Burnham and Anderson 2002). Additionally, proportion of explained variance (R-squared) from fixed effects of the models was calculated and used to support the selection in the case that AIC from models were similar. Finally, we assessed the performance and whether our selected model was a good predictor of the average number of laid eggs by *Ae. aegypti* during the third sampling season (November 2011-May 2012). Coefficient of determination (R^2) was calculated to assess the relationship between the values observed in the third sampling season and those estimated by the model in order to validate it.

3. Results

3.1. Entomological data and temporal analysis

A total of 268,874 *Ae. aegypti* eggs were collected during the three sampling seasons, including 101,278 in the first sampling season, 65,640 in the second and 101,956 in the third sampling season. The average maximum and minimum temperatures were similar in the three sampling seasons, 32.6°C and 12.5°C, respectively. In Figure 2, a similar pattern can be observed in the three seasons when after several weeks with minimum temperatures above 15°C the oviposition peaks were recorded. In addition, it is observed that in later weeks when the minimum temperature is below 15°C the oviposition activity begins to decrease. Precipitation was greater in the first sampling season (758.5mm) while in the latter two it was less than 500mm. Relatedly, it is important to highlight that in November of the first and third sampling seasons there were higher rain averages per week (34mm and 29mm, respectively) than in November of the second (17mm). During the first sampling season, the maximum peak of oviposition activity was observed five weeks after that the highest maximum (38.8°C) and minimum (20.7°C) temperatures were registered. In addition, precipitation was the highest three weeks prior to the maximum peaks of *Ae. aegypti* oviposition activity, and humidity showed a similar pattern. In the second sampling season there was not a noticeable peak of number of eggs; egg counts remained between 3000 and 6000 for the majority of the season. During the third season, a remarkable maximum of oviposition activity occurred with maximum temperatures above 30°C and minimum temperature between 9.3°C and 18.8°C during the previous weeks. Furthermore, large rainfalls and increased humidity occurred prior to the maximum of oviposition.

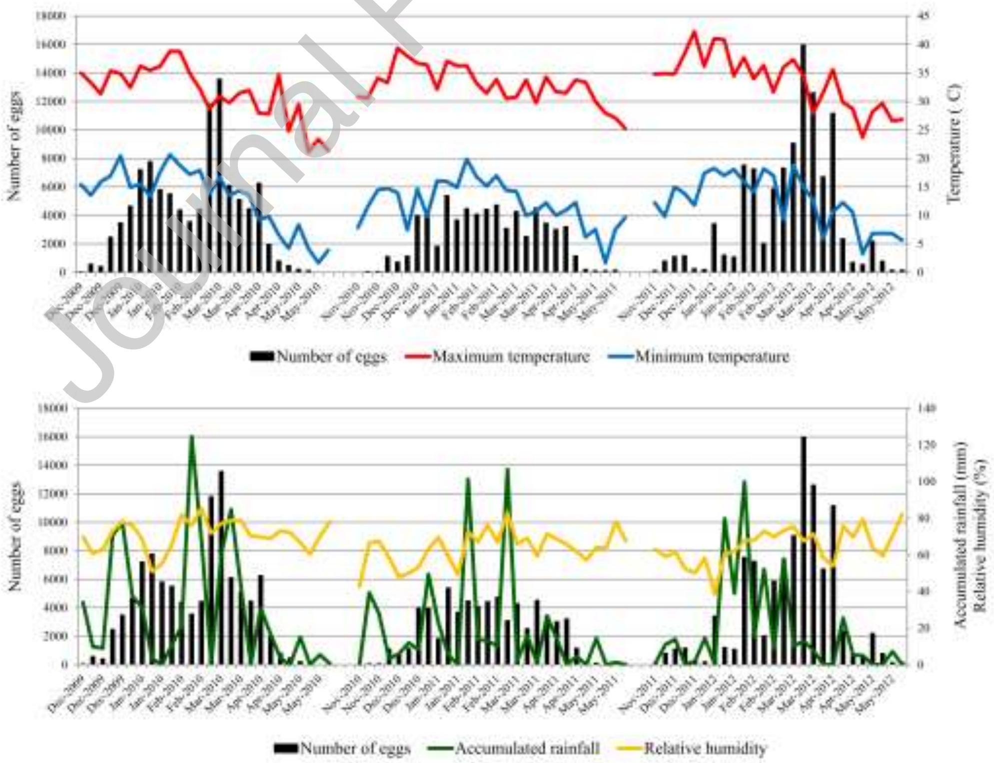

Fig 2. Fluctuation of egg number and meteorological variables from December 2009 to May 2012, in Córdoba city (Argentina).

3.2. Development of the Aedes aegypti oviposition model

The explanatory variables that were selected to fit the models are shown in Table 2 along with their best time lag and coefficient of correlation with the response variable. According to the analysis, the most relevant variables, as determined by the magnitude of their correlation coefficients, were: **VP(t-4,t-1)** mean vapor pressure, **Tm(t-7,t-1)** minimum temperature, **RAIN(t–4,t–1)** accumulated rainfall, **LAI(t-1)** and **EVI(t-3)** vegetation index.

Table 2. Variables used to develop the GLMM that best correlated with the response variable, their respective correlation coefficients, and the associated p-values.

Explanatory variables	**Correlation coefficients**	**p-values**
VP(t-4,t-1)	0.886	0.000
Tm(t-7,t-1)	0.835	0.000
RAIN(t-4,t-1)	0.767	0.000
LAI(t-1)	0.746	0.000
EVI(t-3)	0.733	0.000
Tr(t-4,t-1)	–0.643	0.000

Tm(t-1)	0.601	0.000
Ph(t-4,t-1)	0.52	0.000
RHr(t-5,t-1)	–0.513	0.000
RHm(t-4,t-1)	0.481	2e-04
RHa(t-3,t-1)	0.45	6e-04
NDVI(t-4)	–0.395	0.003
TM(t-1)	0.264	0.054

NDVI(t-4): mean NDVI from the week number 4 before the sampling week; **EVI(t-3)**: mean EVI from the week number 3 before the sampling week; **LAI(t-1)**: mean LAI from the week immediately prior to the sampling week; **Tm(t-1)**: minimum temperature reached during the week immediately previous to the sampling week; **Tm(t-7,t-1)**: minimum temperature reached during the 7 weeks immediately previous to the sampling week; **TM(t-1)**: maximum temperature reached during the week immediately previous to the sampling week; **Tr(t-4,t-1)**: thermal amplitude from the 4 weeks immediately previous to the sampling week; **RAIN(t-4,t-1)**: accumulated rainfall in 4 weeks immediately previous to the sampling week; **RHm(t-4,t-1)**: minimum relative humidity reached during the 4 weeks immediately previous to the sampling week; **RHa(t-3,t-1)**: mean relative humidity reached during the 3 weeks immediately previous to the sampling week; **RHr(t-5,t-1)**: amplitude of relative humidity from the 5 weeks immediately previous to the sampling week; **VP(t-4,t-1)**: mean vapor pressure obtained during the 4 weeks immediately previous to the sampling week; **Ph(t-4,t-1)**: accumulated light hours in 4 weeks immediately previous to the sampling week.

The obtained models are shown in Table 3 with the null model M1 (AIC = 406.5). The explanatory variables that were included in the models were significant and multicollinearity was not found. The best model M2 (AIC = 332.2) is (Eqn 1):

$$\mathrm{Log}(\mathbf{O(t)}) = 2.238 + 0.537 * \mathbf{EVI(t\text{-}3)} + 1.22 * \mathbf{VP(t\text{-}4,t\text{-}1)} - 0.403 * \mathbf{RAIN(t\text{-}4,t\text{-}1)} + \\ + 0.263 * \mathbf{Ph(t\text{-}4,t\text{-}1)} - 0.546 * \mathbf{VP(t\text{-}4,t\text{-}1)} * \mathbf{Ph(t\text{-}4,t\text{-}1)} \quad (1)$$

where **O(t)** is the average number of *Ae. aegypti* eggs per week, **EVI(t-3)** is the mean Enhanced Vegetation Index from the week number 3 before the sampling week, **VP(t-4,t-1)** is the mean vapor pressure obtained during the 4 weeks immediately previous to the sampling week, **RAIN(t-4,t-1)** is the accumulated rainfall in 4 weeks immediately previous to the sampling week and **Ph(t-4,t-1)** is the accumulated light hours in 4 weeks immediately previous to the sampling week.

Fitted curves of the effects of each one of these variables is shown in the Figure 3. Based on this model, a positive relationship was observed between **EVI(t-3)** vegetation index and the response variable **O(t)** (Fig 3A). Meanwhile, the interaction (**VP(t-4,t-1)***Ph(t-4,t-1)**) between mean vapor pressure of water and photoperiod, as well as **RAIN(t-4,t-1)** accumulated rainfall, were negatively associated with the number of eggs **O(t)** (Fig 3B-D). According to the model obtained, the average number of eggs **O(t)** increased 1.71 for each incremental unit in **EVI(t-3)** vegetation index and it decreased 0.668 for each millimeter of **RAIN(t-4,t-1)** accumulated rainfall that was added. Regarding to the interaction (**VP(t-4,t-1)*Ph(t-4,t-1)**) between mean vapor pressure of water and photoperiod, it was observed that the effect of the **Ph(t-4,t-1)** photoperiod was positive on the average number of eggs **O(t)** at low values of **VP(t-4,t-1)** mean vapor pressure of water, while it was negative at high values of **VP(t-4,t-1)** mean vapor pressure of water; besides **VP(t-4,t-1)** mean vapor pressure of water had a positive relationship with the response variable **O(t),** however the slope changed at different values of the **Ph(t-4,t-1)** photoperiod observing a stronger relationship at low values. The coefficient of determination (R-squared) calculated indicates that the fixed effects of model M2 explain 93% of the variance of the average number of *Ae. aegypti* eggs per week.

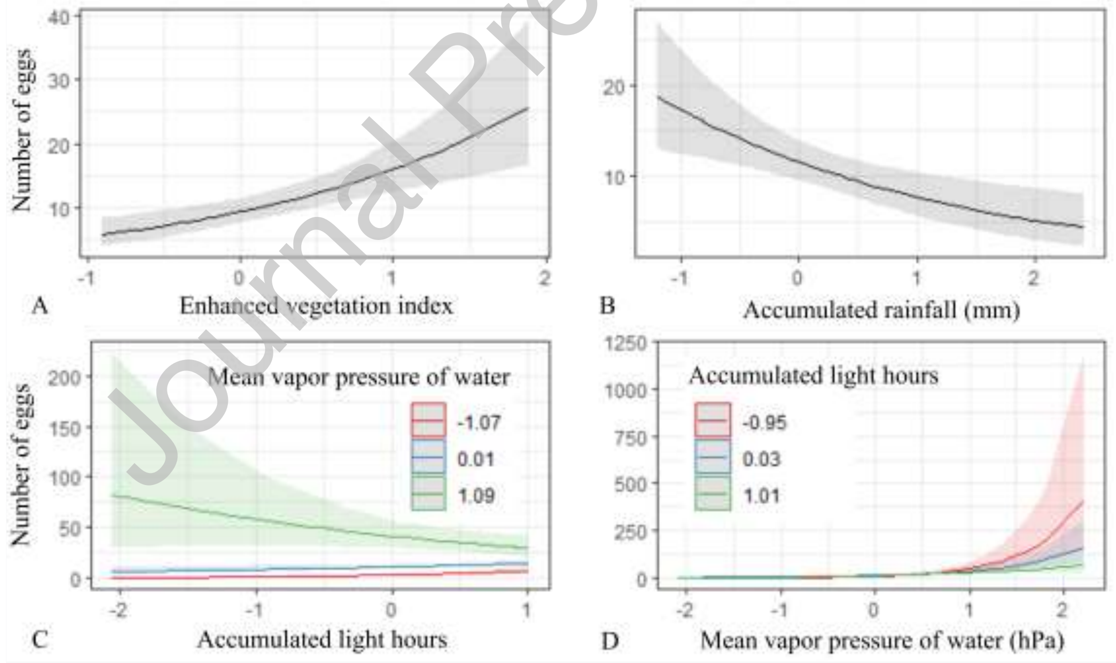

Fig 3. Fixed effects: curves predicted by the selected model M2. The X axes acquire negative and positive values because the explanatory variables are standardized.

Table 3. Additional information about the developed models.

Model	Variables	Estimates	p-value	95% confidence interval	Standard error	AIC	R^2
M1	Intercept	2.21	4.27e-07	1.23 ; 3.109	0.437	406.5	
	M (Months)			0.954 ; 2.495			
M2	Intercept	2.238	< 2e-16	1.988 ; 2.434	0.108	332.2	0.928
	EVI(t-3)	0.537	4.05e-05	0.275 ; 0.814	0.131		
	VP(t-4,t-1)	1.22	1.27e-15	0.923 ; 1.539	0.153		
	RAIN(t-4,t-1)	-0.403	0.002	-0.656 ; -0.146	0.128		
	Ph(t-4,t-1)	0.263	0.019	0.033 ; 0.518	0.112		
	VP(t-4,t-1)*Ph(t-4,t-1)	-0.546	5.23e-05	-0.822 ; -0.278	0.135		
	M (Months)			0.000 ; 0.416			
M3	Intercept	2.343	< 2e-16	2.058 ; 2.59	0.124	331.3	0.894
	EVI(t-3)	0.853	5.66e-07	0.503 ; 1.178	0.171		
	VP(t-4,t-1)	1.33	< 2e-16	1.062 ; 1.652	0.149		
	Tr(t-4,t-1)	0.317	0.003	0.106 ; 0.52	0.105		
	EVI(t-3)*VP(t-4,t-1)	-0.77	9.10e-08	-1.058 ; -0.492	0.144		

	M (Months)			0.093 ; 0.596			
M4	Intercept	2.112	< 2e-16	1.778 ; 2.378	0.145	344.2	0.856
	EVI(t-3)	0.488	0.003	0.171 ; 0.821	0.162		
	VP(t-4,t-1)	1.267	4.18e-16	0.973 ; 1.596	0.156		
	RHa(t-3,t-1)	-0.404	0.0001	-0.613 ; -0.195	0.106		
	M (Months)			0.134 ; 0.656			
M5	Intercept	1.947	< 2e-16	1.522 ; 2.288	0.186	350	0.836
	EVI(t-3)	0.762	2.98e-05	0.409 ; 1.129	0.183		
	Tm(t-7,t-1)	1.364	4.52e-11	0.972 ; 1.797	0.207		
	Tr(t-4,t-1)	0.293	0.036	0.016 ; 0.565	0.14		
	M (Months)			0.245 ; 0.868			

EVI(t-3): mean EVI from the week number 3 before the sampling week; **VP(t-4,t-1)**: mean vapor pressure obtained during the 4 weeks immediately previous to the sampling week; **RAIN(t-4,t-1)**: accumulated rainfall in 4 weeks immediately previous to the sampling week; **Ph(t-4,t-1)**: accumulated light hours in 4 weeks immediately previous to the sampling week; **Tr(t-4,t-1)**: thermal amplitude from the 4 weeks immediately previous to the sampling week; **RHa(t-3,t-1)**: mean relative humidity reached during the 3 weeks immediately previous to the sampling week; **Tm(t-7,t-1)**: minimum temperature reached during the 7 weeks immediately previous to the sampling week.

In addition to the **EVI(t-3)** vegetation index and **VP(t-4,t-1)** mean vapor pressure, we developed other models that incorporated variables such as **Tr(t-4,t-1)** temperature range, **RHa(t-3,t-1)** mean relative humidity and **Tm(t-7,t-1)** minimum temperature. According to these models, the average number of eggs **O(t)** increased 1.37 and 3.91 for each unit of increase in **Tr(t-4,t-1)** temperature range and **Tm(t-7,t-1)** minimum temperature respectively, and decreased 0.668 when **RHa(t-3,t-1)** mean relative humidity increased one unit.

Data from third sampling season were used to validate the model, which resulted in a R^2 coefficient of determination of 0.7 between the *Ae. aegypti* oviposition activity observed and the activity predicted by the model M2 (Fig 4).

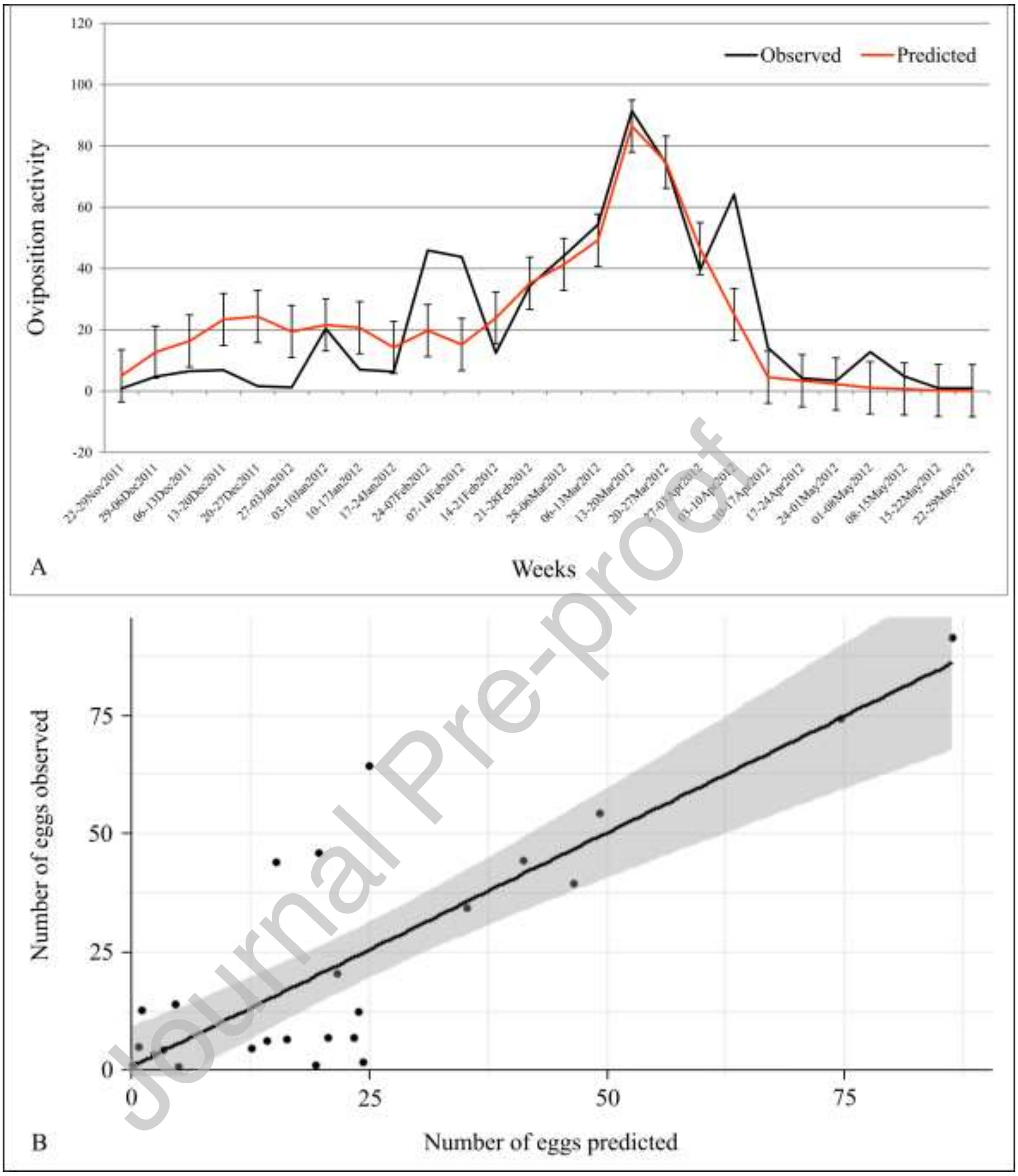

Fig 4. (A) Oviposition activity, measured as the average number of *Aedes aegypti* eggs per week, observed and predicted by the best model obtained in the third sampling season in Córdoba city (Argentina). Confidence intervals are shown on predicted data. (B) Scatter plot based on the average number of *Aedes aegypti* eggs per week observed and predicted by the model selected from the third sampling season.

4. Discussion

In this study we developed several models to forecast temporal *Ae. aegypti* oviposition activity fluctuation in relationship to environmental variables determined from satellite vegetation and meteorological data in the temperate city of Córdoba, Argentina. During the second sampling season, the amount of eggs was 35% lower than the first and third, which could be due to diminished rains during November of the second season. In fact, several studies note the occurrence of greater rainfall in the months prior to peaks in mosquito oviposition activity as well as for peaks in dengue cases (Vezzani et al. 2004, Rubio-Palis et al. 2011, Estallo et al. 2015). Indeed, rainfall could be an important factor affecting the availability and suitability of containers that act as potential breeding sites (Micieli and Campos 2003). The difference in the number of eggs found between sampling seasons in our study could be due to a combination of factors like the amount and distribution of rainfall that condition the number of available sites where females lay eggs. This could influence the number of eggs remaining for the next sampling season as well and therefore subsequent vector activity because vectors persist in Córdoba city through the cold season only through unhatched eggs hatch when the environment becomes favorable in the warmer season (Dominguez et al. 2000, Estallo et al. 2020).

This study provides strong evidence of the importance of vegetation and meteorological variables in predicting *Ae. aegypti* oviposition activity. Vegetation index with a lag of 3 weeks was found to be one of the most important variables for egg prediction, showing a positive relationship and fluctuating in a similar manner to oviposition activity. This relationship has also been observed in the sub-tropical climatic conditions of northern Argentina with a lag of 21 weeks in the NDVI (Estallo et al. 2016). Temporal variation in temperature, humidity and precipitation, affects vegetation development (Huete et al. 2002, Liu et al. 2015). This suggests that increases in vegetation increment could be due to humidity and precipitation in the near past, which itself could be followed by an increase in vector activity due to increases in habitat for mosquitos.

In Córdoba city, which has a temperate climate and cold winters without vector activity (Estallo et al. 2020), larval development and then the presence of adults during the favorable season depends mainly on the activity of the previous season, eggs laid in containers late in previous season, and precipitation in a new favorable season to induce hatching. The negative relationship between the average number of eggs and accumulated rainfall in the previous 4 weeks found here could be explained by preference of females for containers that are not filled completely with water. That is, if containers are full due to the abundant rains, females may avoid those containers. In Malaysia, *Ae. albopictus* females were found to prefer to lay eggs in half-filled containers, whereas overflowing containers acted as a repellent for gravid females. This is because the rains tend to fill the containers and spill the water that is in them, and consequently this could eliminate the juveniles that are developing in those breeding sites (Dieng et al. 2012). Furthermore, the negative relationship found in our study could be due to availability of nearby breeding sites that are more favorable following rain events, leading to the distribution of eggs among all the available breeding sites, and fewer eggs in the ovitraps. On the other hand, it may happen that when rain is scarce, the breeding sites are also reduced and as consequence the females lay eggs in the ovitraps, which leads us to detect a greater number of eggs in them.

In the present study, we found important relationships between temperature and oviposition activity. First, we found minimum temperature reached during the seven weeks prior to collection of eggs of greater importance to vector activity than the maximum temperature from one week prior of egg collection. A minimum temperature of 15°C seems to define a threshold for the oviposition activity: when the temperature is above this value the number of eggs increases perhaps due to a greater number of active females. This highlights the role of minimum temperature in predicting oviposition activity, which is in agreement with previous studies in temperate Buenos Aires and Córdoba area (Dominguez et al. 2000, Vezzani et al. 2004). It is further confirmed in Australia, where Kearney et al. (2009) found that cold tolerance is one of the most important factors that limit the presence of adults and larvae, and other studies point to a general linear tendency between water temperature and development rate for eggs and juveniles (Eisen et al. 2014). Additionally, Rowley and Graham (1968) determined that sustained flight of *Ae. aegypti* in experiments occurred in a temperature range between 15°C and 32°C, although the flight was possible at extreme minimum temperatures of 10°C with a minimum performance as measured by duration and distance.

Also of importance was the thermal amplitude from the 4 weeks prior to the collection of eggs, which showed a positive relationship with oviposition activity, which is in contrast to results of some other studies such as one in Thailand where temperature fluctuation was found to have a negative effect on *Ae. aegypti* (Carrington et al. 2013). This difference could be due to influences of other variables of our model that are not present in studies aimed at understanding the effect of temperature fluctuation in isolation.

Photoperiod in the 4 weeks prior to eggs collection was not one of the main variables correlated explain oviposition activity in our study; however, it was important in association with variables like EVI vegetation index, vapor pressure and accumulated rainfall, and it showed a significant effect on eggs in interaction with mean vapor pressure of water obtained during the previous 4 weeks. The importance of the photoperiod on oviposition activity was observed in another study made in Córdoba city (Dominguez et al. 2000), although it had no significant effect on the vector in a subtropical area of Argentina (Estallo et al. 2015). This contrast in results among studies could be due to differences in photoperiod variation at different latitudes. On the other hand, a positive effect of mean vapor pressure of water in the previous 4 weeks on the average number of eggs was found here, although this relationship was stronger at low photoperiod values than at high values. Similarly, Estallo et al. (2015) found a positive relationship between *Ae. aegypti* egg number and vapor pressure of water in subtropical Argentina, showing a decrease in eggs with decreases in vapor pressure. Perhaps this positive association is because vapor pressure of water is closely related to humidity, which has an important positive effect, in interaction with temperature, on oviposition rate and adult survival (Costa et al. 2010). In our work, although relative humidity showed a low correlation value, it was important enough to be entered into one of our models. Relatedly, there are works that point out the importance of the relative humidity on the vector activity despite its low correlation, and when all conditions are considered, the activity of vectors is low when the relative humidity is not adequate, such that relative humidity may be acting as a limiting factor (Micieli and Campos 2003, Costa et al. 2010, Estallo et al. 2015).

The average number of predicted eggs in the third season showed underprediction and overprediction compared with the number of eggs observed, which may be due to local socio-ecological conditions that control the survival of the vector and were not studied here. Despite this, our model predictions explain a good percentage of the variance of the number of observed eggs, which indicates that the predictive model is reliable.

Predictive models are an important tool in temperate cities, which have marked seasonality since they can help vector surveillance over time. These models are useful and necessary to guide control strategies that aim mainly to reduce vector abundance. In Córdoba city, *Ae. aegypti* larval monitoring is carried out through searching for potential mosquito breeding sites, locating larvae, taking samples in order to monitor the vector, and subsequently destroying these breeding sites during vector activity months. In Estallo et al. (2020), the number of *Ae. aegypti* eggs was positively correlated with larval abundance (measured as percentage of neighborhoods with *Ae. aegypti* larvae) found in the following month in Córdoba city. Therefore, the model obtained in this study could help predict both the increase and the peak of oviposition activity in the city that would lead to an increase in the number of larvae in subsequent weeks. Being able to predict oviposition activity in the short term will be useful to guide and reinforce the controls focused on the elimination of larvae that would ultimately lead to population reduction of the vector. These models are also likely useful for other temperate regions similar to Córdoba city with similar patterns in climate These models will allow mosquito control authorities to anticipate the beginning of larval activity, and start vector control campaigns earlier, and assist local public health authorities in preparing for seasonal outbreaks of dengue and related arboviruses.

Declaration of interest

The authors report no conflict of interest.

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: