

Spatial distribution pattern of oviposition in the mosquito *Aedes aegypti* in relation to urbanization in Buenos Aires: southern fringe bionomics of an introduced vector

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Abstract. The distribution of *Aedes aegypti* (L) (Diptera: Culicidae) oviposition in Buenos Aires City is spatially heterogeneous. Oviposition activity was monitored for a year with a grid of 279 traps at 850-m intervals that were serviced weekly. Geostatistics were used for the spatial analysis and generalized linear regression to model oviposition as a function of demographic and environmental variables. The proportion of weeks infested and the total number of eggs showed spatial continuity and were higher in areas that had higher densities of houses and were closer to industrial sites; they were lower in areas with higher human populations or higher densities of flats. When all sites were considered, the spatial structure showed a strong trend, but after regression, the residuals presented lower spatial dependence. When only infested sites were considered, the oviposition variables were spatially autocorrelated and the regression residuals showed little or no spatial dependence. The spatial pattern of *Ae. aegypti* oviposition in a highly urbanized city such as Buenos Aires seems to be related to the urbanization gradient. These urban environments might present different resource availability or continuity between patches of resources.

Key words. *Aedes aegypti*, demography, dengue vector, geostatistics, GIS, mosquito bionomics, mosquito distribution, mosquito oviposition, ovitrap, spatial analysis, urbanization, Buenos Aires, Argentina.

Introduction

The southern limit of the world distribution of *Aedes aegypti* (L) is ~ 35° south, along the 10°C isotherm of July (Christophers, 1960). Buenos Aires City is located near this limit (Sabattini *et al.*, 1998), which might facilitate the identification of ecological factors that limit urban yellow fever and dengue virus vector distribution on the urban scale. The heterogeneous distribution of *Ae. aegypti* in cities has been described as a cause of abundance estimation difficulties (Tun-Lin *et al.*, 1996). It has been associated with economic levels (Tinker, 1964) and humidity heterogeneities in the U.S.A. (Fink *et al.*, 1998). We used ovitrap monitoring of *Ae. aegypti* in Buenos Aires City to

show heterogeneous spatial and temporal patterns in its distribution. Downtown neighbourhoods to the east showed lower levels of infestation than the rest of the city and adult activity was detected only between October and May, peaking in February and March. Both spatial and temporal annual patterns were found to be repeated during the 3-year study (Carbajo *et al.*, 2004). The analysis of the spatial pattern of *Ae. aegypti* oviposition in relation to environmental variables at the city scale of vector-borne diseases is typically limited to vector distribution and habitat preferences (Kitron, 1998). Study of the association of *Ae. aegypti* distribution patterns with environmental variables at the city scale may help us understand the relationship between oviposition and adult abundance.

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In ecological studies, depending on the scale of study, observations are not independent nor distributed at random as conventional statistics assume (Legendre, 1993). It is common to find that observations tend to be more similar when measured at closer locations (spatial dependence). Legendre (1993) differentiates between two types of spatial dependence: true gradients (trends) and spatial autocorrelation. The former can be expressed as a function of absolute co-ordinates plus an error independent of location; the latter needs to consider relative position, as the value of a site is partly determined by its neighbours. The distribution of living beings might show one of these spatial dependencies due to associations with the environment or to contagious biotic processes, such as reproduction, death, predation, competence and so on.

The objective of this study was to analyse the spatial pattern of *Ae. aegypti* oviposition activity in Buenos Aires City and its relationships with demographic and environmental variables. The results should help to determine whether the pattern follows a true environmental gradient or is due to spatial autocorrelation.

Materials and methods

Study site

Buenos Aires City, the capital of Argentina, lies on the de la Plata River, which has an estuary approximately 50 km wide (Fig. 1). The city has a diameter of ~16 km and covers an area of 200 km². It has a population of 3 000 000 and is surrounded by urban areas with a total population of nearly 9 000 000 inhabitants. Buildings range from residential houses of low height to high-rise multistorey buildings, and are mainly constructed of bricks and concrete. The city is situated at 34° 35' south, 58° 29' west and is 25 m above sea level. The climate is temperate-humid with four seasons, mean annual rainfall of 1076 mm, mean annual temperature of 17.4°C and mean annual wind speed of 12 km/hour (Instituto Geográfico Militar, 1998).

Data collection

Oviposition activity was monitored in the city from July 1999 to June 2000 with oviposition traps (Fay & Eliason, 1966). Each trap consisted of a black-painted, glass flask filled with water up to a third of its volume, in which stood a small wooden paddle with the rough side pointing to the centre of the flask. A grid of 279 fixed sites (at 850-m intervals) with one trap in each was used to cover the city (Fig. 1). The traps were laid on public pavements, at the base of homogeneous plant cover in shade. They were serviced weekly, cleaned, refilled and the paddle replaced. A trap was considered as non-operative for a week if it was absent, found destroyed or without a paddle. The paddles were inspected by stereomicroscope in the laboratory and the *Ae. aegypti* eggs were counted. A trap was considered to be infested in a week when at least one egg was found. The variables measured at each site were: the proportion of weeks infested by *Ae. aegypti* (PI = weeks infested/operative weeks) during the main season of adult infestation (October to May) and the total number of eggs (TE = total sum of weekly egg counts during

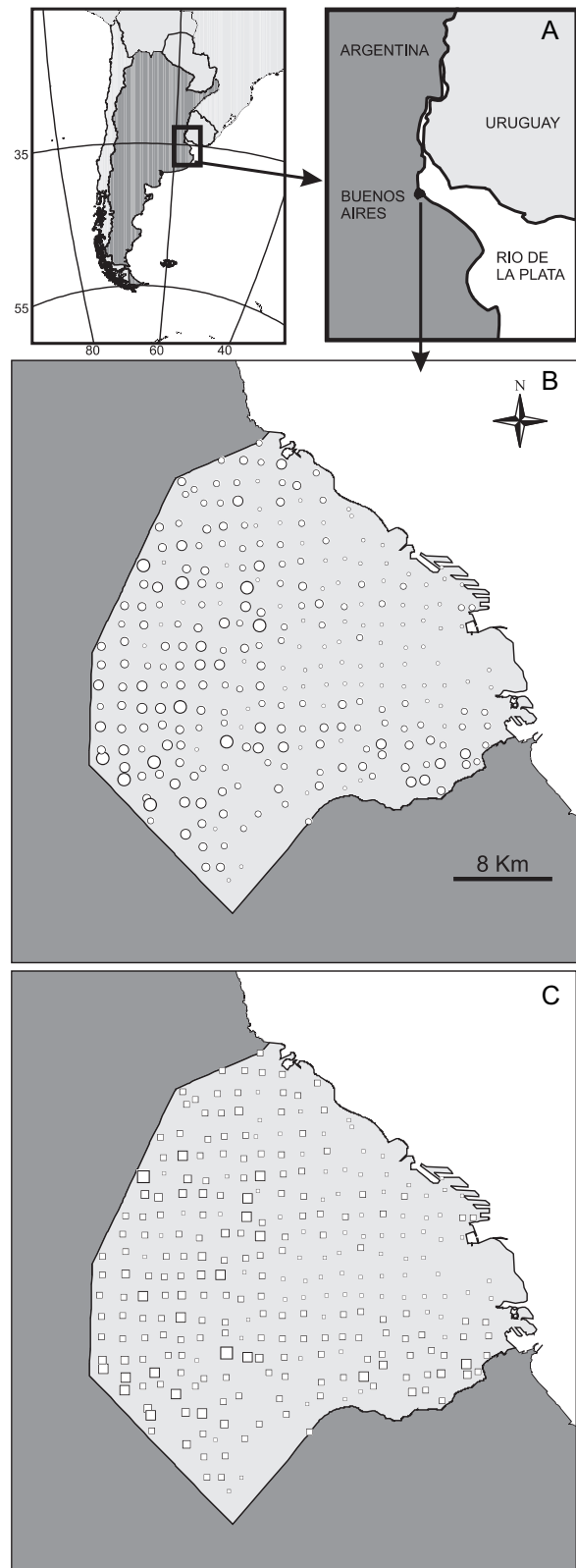


Fig. 1. (A) Maps of Buenos Aires showing (B) the proportion of weeks infested with *Ae. aegypti* (PI), and (C) the total number of eggs (TE). Symbol sizes are proportional to the PI or TE measured at each site.

the sampling period). The locations of the sites were digitized with an approximate error of 5 m in a geographical information system (GIS; ARCVIEW 3.1; ESRI,). The geographical database included city blocks, pavement, parks (polygon layers), avenues (i.e. main multi-lane thoroughfares), streets, rivers (lines), and altitude measurements (points).

Demographic and environmental digital data recorded for each block included: number of inhabitants, number of employees, number of houses (individual residences) and number of flats (residences in multistorey buildings) (Instituto Nacional de Estadísticas y Censos, 1991). The locations of main industrial sites were recorded as points. Industrial sites in the city typically occupy areas smaller than 1 hectare, and many have become abandoned in the last decade. Only three types of industries were considered: metallurgy, animal hide tanning and refrigeration industries (the latter two are associated with animal slaughterhouses). Other industrial sites were excluded as they seemed less likely to house potential breeding containers due to commercial requirements for cleanliness (e.g. petrol stations, food production/distribution, textiles and chemicals).

The following layers of explanatory variables were generated by GIS: density of residences (houses and flats); inhabitants per residence; population density; employee: population ratio; density of flats; density of houses; proportion of the surface covered by vegetation (i.e. parks or plazas, but not small gardens); distance to avenues; distance to industrial sites, and ground altitude. Contour lines were interpolated by 'kriging', a geostatistical approach to modelling, which assumes a normal distribution of data points. Instead of weighting nearby data points by some power of their inverted distance, kriging relies on the spatial correlation structure of the data to determine the weighting values; the correlation between data points determines the estimated value at an unsampled point. Densities were expressed per 100 m² and converted into a grid of 10 × 10-m cell size that covered the whole city. The mean of the variables in 100-m and 300-m radius buffers around the site were calculated. Distances and altitude were measured at the exact location of the sites.

Statistical analysis

The use of spatial statistics in the study of disease has been reviewed elsewhere (Marshall, 1991). According to Cressie (1993) there are three main branches of spatial data analysis: lattice, geostatistics and point pattern. Lattice analysis deals with spatial data for whole areas with information about the whole surface under study (e.g. satellite images or political subdivided zones). Geostatistics mainly uses data for spatially continuous variables sampled at several locations and allows for additional data to be obtained by further sampling. In point pattern analysis, the main interest is the location of events and their distribution, but the location of all the elements is required (e.g. vegetation census data). We considered that our data would be better modelled by geostatistics; it was assumed that the proportion of weeks infested (PI) and total number of eggs (TE) per site were spatially continuous variables and that trap sites represented a sample of the spatial distribution pattern. Geostatistics

have been previously used in illness mapping (Carrat & Valleron, 1992; Srividya *et al.*, 2002) and in entomological and vector-borne disease studies (Brenner *et al.*, 1998; Focks *et al.*, 1999).

The semivariogram was used to study the spatial dependence of *Ae. aegypti* oviposition. This tool recognizes spatial variability on both the large scale (spatial trend) and the small scale (spatial autocorrelation) (Cressie, 1993). The semivariogram describes how sample data are related with separation distance and direction. It plots $\lambda(h)$, one-half the average squared difference between paired data values, vs. h , the distance separating the points. When there is spatial dependence the semivariogram increases with h . If it does so without levelling off (unbounded), this indicates the presence of a trend or gradient, which might be due to a gradient in some environmental variable (Jongman *et al.*, 1987; Rossi *et al.*, 1992). When it levels off, this indicates the presence of autocorrelation, or the tendency of close pairs to be more similar than far away ones. Sometimes the trend can obscure the autocorrelation and must be removed. The value of $\lambda(h)$ when it levels off is called the 'sill' and the value of h the 'range'. The range represents the maximum distance at which there is spatial dependence, and beyond it observations become independent. The intercept of the variogram at $h = 0$ must be zero, but is sometimes higher. It is called the 'nugget' and responds to sampling error or spatial dependence acting at separations lower than that of the sampling. Spatially continuous variables show low nuggets. When the semivariogram is completely horizontal (pure nuggets), this indicates a lack of spatial dependence at the sampling scale. The same happens at h higher than the range when a sill is present. When the semivariograms are different for some directions, the spatial structure is said to be 'anisotropic'; if they are equal for all directions it is called 'isotropic' and is only a function of separation distance. As the semivariogram is estimated for discrete separation classes ('lags'), a model needs to be fitted to estimate the values for all h . Standardized semivariograms (λ/σ^2) were utilized to describe the spatial structure of individual variables. In this type of variogram one unit equals the variance, so the sill would approximate 1 as it estimates the total sample variance; the nugget estimates the proportion of the variance that corresponds to random noise. The difference between the sill and nugget represents the proportion of the total variance that can be modelled as spatial dependence (Rossi *et al.*, 1992). The relationship between this difference and the sill: (sill-nugget)/sill, was used to compare the degree of spatial dependence. We used the robust modification of semivariograms (Cressie & Hawkins, 1980; Cressie, 1993), a lag of 750 m up to half the maximum separation distance and a minimum of 50 pairs of points per lag estimate. Four directions were considered to account for anisotropy: 0°, 45°, 90° and 135° (the north-south meridian corresponded to 0°). The semivariogram was fitted by weighted least squares. Analysis was carried out with S-PLUS 6 software with Spatial Statistics and ARCVIEW add-ons (Insightful Corp.).

Two procedures were carried out to check whether large-scale trends obscured autocorrelation. Firstly, a subset was made excluding the sites not infested by *Ae. aegypti* (PIo and TEo). Secondly, in all datasets the response variables PI, PIo,

TE and TEo were modelled as a function of demographic and environmental explanatory variables with multiple regression and the residuals studied with spatial analysis as described above (Bailey & Gatrell, 1995).

Regression models

Generalized linear models (GLMs) (Nelder & Wedderburn, 1972; McCullagh & Nelder, 1989) were used to find the best model that described the response variables (S-PLUS 6; Insightfull Corp.). These GLMs permit a wider range of models than linear regression, which assumes normal error distributions and constant variance, and are preferable to the log-transformation of the response variable when the distribution is very skewed (Wilson *et al.*, 1996; Wilson & Grenfell, 1997). The response variables PI and PIo vary between 0 and 1, so we assumed a binomial distribution of errors, a variance equal to $\mu(1-\mu)$ and applied a logistic link function. The variables TE and TEo consist of count data, so a Poisson distribution with variance equal to μ and a log link were used (Crawley, 1993). To account for over-dispersion, the model was rescaled and the scale parameter estimated by pseudo-likelihood (McCullagh & Nelder, 1989; Venables & Ripley, 1999). Each explanatory variable was tested in turn for significance, and only those significant at the 1% level were included in the model. Two-tailed *t*-tests were carried out for parameter estimates (Crawley, 1993), parameter/SE with error degrees of freedom (278 and 193). The variable contributing to the largest significant change in deviance from the null model was then selected and fitted. To avoid co-linearity, the correlation between pairs of explanatory variables was calculated; when it surpassed 50% the one that explained less deviance was excluded from the model. The variables with estimated parameters that correlated more than 25% were excluded in a similar manner. Finally, the geographical co-ordinates (absolute position) were checked for any further explanatory power to verify that no spatial trend was left (Legendre, 1993). Residual analysis was conducted to select the best models. The standardized residuals were plotted against fitted values (to check lack of fit of the residuals) and normality checked with quantile–quantile plots (data quantiles against normal quantiles). The regression parameters were recalculated using jack-knife resampling to check the effects of influential observations.

Results

Ae. aegypti was detected in 69.5% of the sites (194/279). The median proportion of weeks infested (PI) during the infestation period was 0.08 (first and third quartiles: 0.00, 0.13; maximum: 0.41). The spatial pattern is shown in Fig. 1. A total of 21 159 eggs were found on 13 674 paddles recovered between July 1999 and June 2000. The total number of eggs per site (TE) median was 30 (first, third quartiles, maximum: 0, 99, 1005). The infested paddles weekly mean number of eggs was 25 and the median was 15 (first, third quartiles, maximum: 6, 32, 230). The correlation between the response variables PI and TE was 0.95 and between PIo and TEo

was 0.86 (Spearman $Z = 15.88$, $P = 0.00$, $n = 279$ and $Z = 11.97$, $P = 0.00$, $n = 194$, respectively).

The variograms of PI and TE showed spatial dependence, as an increase in separation distance corresponded with increased dissimilarity, but showed no definite sill, suggesting the existence of a trend. They differed in direction, indicating anisotropy. The nugget was around 0.3 standardized semivariance for PI and 0.15 for TE (Fig. 2). The subset of sites with records of *Ae. aegypti* showed less spatial dependence and higher nuggets for both variables (PIo and TEo). The PIo variograms were flat except for the 45° and 90° directions, which showed a nugget around 0.5 and a subtle plateau (Fig. 3). The TEo showed spatial dependence and plateaux in all directions but 45°. Both variables showed higher spatial dependence in the 90° direction (PIo 45%, TEo 46%). The directions that showed spatial dependence levelled off, indicating autocorrelation of the response variables (Fig. 3).

The variograms of the environmental and demographic variables also showed anisotropy (Fig. 4). Strong spatial structure

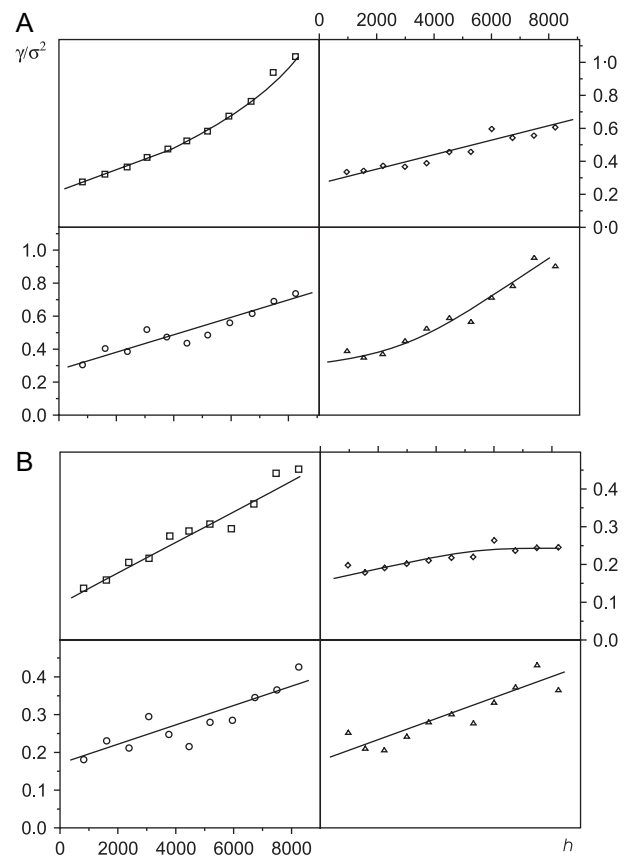


Fig. 2. Anisotropic standardized semivariograms of the response variables for all sites. (A) Proportion of weeks infested by *Ae. aegypti*. (B) Total number of eggs. Directions of anisotropy are indicated by symbols: circles represent north–south (0°); triangles represent north–east–south–west (45°); squares represent east–west (90°), and rhombi represent north–west–south–east (135°). The ordinates show the standardized semivariance (γ/σ^2) and abscises the separation distance between points (h) in metres. Plotted semivariograms were fitted by weighted least squares.

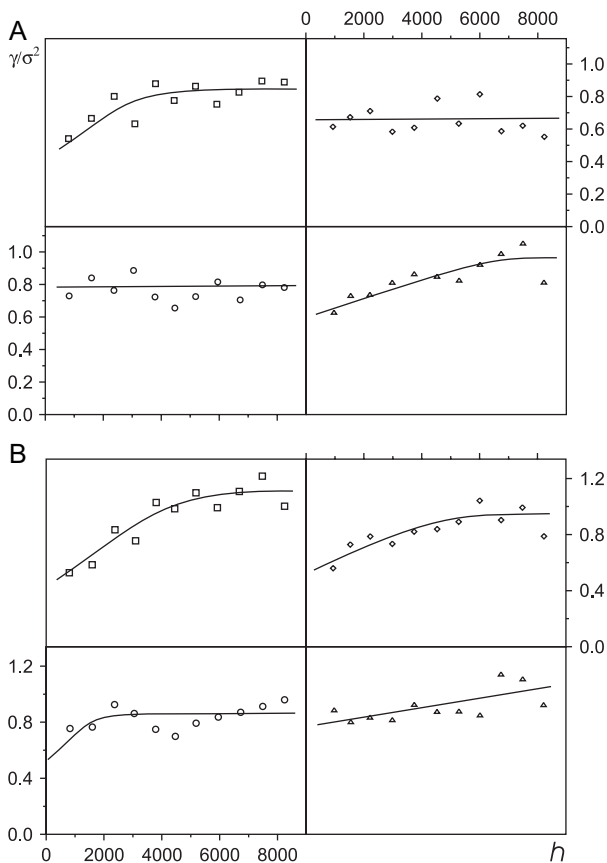


Fig. 3. Anisotropic standardized semivariograms of the response variables for infested sites. (A) Proportion of weeks infested by *Ae. aegypti*. (B) Total number of eggs. Directions of anisotropy are indicated by symbols: circles represent north–south (0°); triangles represent north–east–south–west (45°); squares represent east–west (90°), and rhombi represent north–west–south–east (135°). The ordinates show the standardized semivariance (γ/σ^2) and abscises the separation distance between points (h) in metres. Plotted semivariograms were fitted by weighted least squares.

and low nuggets were observed for altitude, distance to industrial sites, vegetation cover, employee ratio, house, flat and population densities. Residence density was equivalent to population density and thus is not shown. Inhabitants per residence showed little spatial structure and distance to avenues showed pure nugget effect. Flat, house and population density variograms showed maximum dependence without levelling off in the north–south and north–east–south–west directions (0° and 45° , respectively), which coincide with the strongest directions of spatial dependence of PI and TE.

All the variables measured at a 100-m radius were correlated with the 300-m variables. Flat density, residence density and population density were also highly correlated. The 300-m variables and flat density were kept for further analysis due to their better explanatory power.

The best GLM for PI and PIo included house density, flat density and distance to industrial sites as explanatory variables.

They accounted for 40.4% and 27.0% of the total deviance, respectively (Table 1). The residuals check showed some remnant trends for PI, but were satisfactory for PIo. The best model for TE also included house density, flat density and distance to industrial sites, but showed very high dispersion. The GLM for TEo included the previous three variables plus distance to avenues as marginally significant. It was necessary to log-transform TEo to make a satisfactory residual check. The models accounted for 37.7% and 27.3% of the total deviance, respectively (Table 2). In all models house density and distance to industrial sites were directly related to infestation, whereas flat density and distance to avenues were inversely related.

Variograms of the PI and TE GLM residuals showed less spatial dependence than the raw data and were also anisotropic (Fig. 5). The nugget was around 0.6 for PI, the spatial dependence was null in the 135° direction (flat variogram); TE showed a nugget of 0.3 and behaved similarly to PI. The variograms of PIo GLM residuals were isotropic and flat around 0.9 standardized semivariance (Fig. 6), indicating the absence of spatial dependence and supporting the regression model assumption of spatial independence (Cliff & Ord, 1973). The variograms of TEo GLM residuals were flat around 1 γ/σ^2 except for 90° , which showed a nugget of 0.8 and a sill of 1, resulting in small spatial dependence (20% of the variance).

Discussion

The spatial pattern of *Ae. aegypti* oviposition could be modelled as a function of urbanization variables. The models were satisfactory for the whole city, which included large areas with no oviposition activity; they included similar explanatory variables for the subset of infested sites. Less oviposition was seen in more urbanized areas (higher flat density or human population density) and more activity in less urbanized areas (high house density or closer to industrial sites). There was also a weak inverse relation to distance to avenues in the number of eggs deposited. The same variables explained the pattern of datasets with and without non-infested sites, indicating that the associations observed were not an artefact of these latter clusters. In Brazil and the U.S.A. the prevalence of *Ae. aegypti* is greater in more urbanized areas (Braks *et al.*, 2003). Our results do not contradict these authors, because Buenos Aires City has a mean population of 15 000 inhabitants/ km^2 and falls into their ‘urban’ category. We worked on a finer scale, considering areas of 300-m radius within the city, and postulate that in highly urbanized and populated cities urbanization levels might influence oviposition and even lower its levels until no activity is detectable.

The whole-city regression model showed a remnant spatial trend in the residuals. The variograms of that trend showed the highest spatial structure in the east–west and north–south directions, which might be caused by the cluster of non-infested sites in the east of the city. This might be due to the inability of the regression model to remove that trend. The exclusion of the non-infested sites was able to remove the trend; when the residuals were further modelled as a function of the urbanization variables no spatial dependence was left at all. This suggests that the oviposition spatial structure was a consequence of the

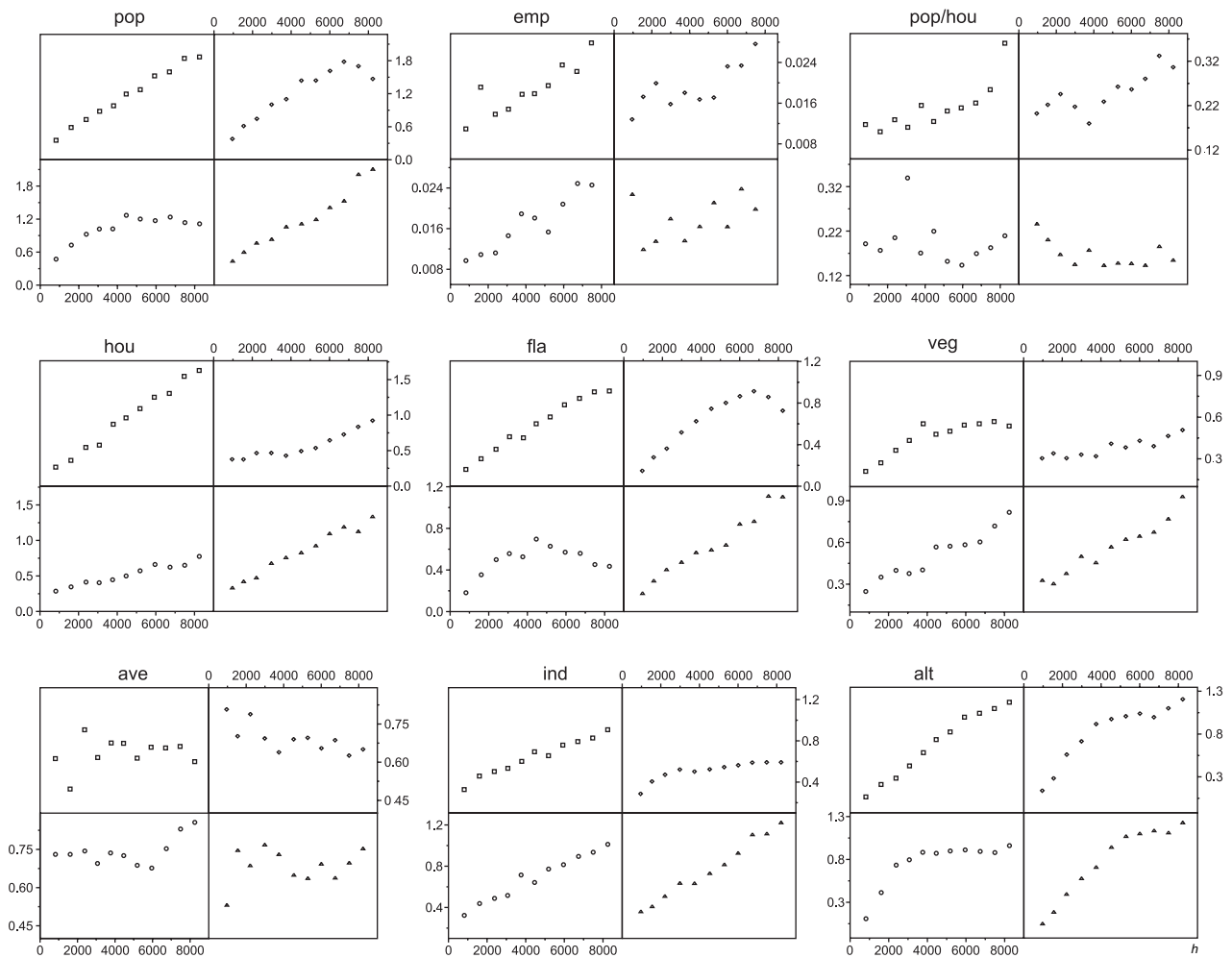


Fig. 4. Anisotropic standardized semivariograms of demographic and environmental explanatory variables in Buenos Aires City. Pop = population density; emp = employees : population ratio; pop/hou = inhabitants per residence; hou = density of houses; fla = density of flats; veg = proportion of surface vegetated; ave = distance to avenues; ind = distance to industrial sites; alt = altitude above sea level. Directions of anisotropy are indicated by symbols: circles represent north–south (0°); triangles represent north–east–south–west (45°); squares represent east–west (90°), and rhombi represent north–west–south–east (135°). The ordinates show the standardized semivariance (γ/σ^2) and abscises the separation distance between points (h) in metres.

spatial structure of urbanization. An exception was the east–west direction of the GLM residuals from the total number of eggs; its variogram showed a definite sill and a range of 2 km. This spatial dependence should be regarded with caution as it was subtle and the nugget was too high. The *Ae. aegypti* oviposition pattern in Buenos Aires might represent a ‘true gradient’ as it was mainly related to the urban environment and not to itself; the similarity between the variograms of house density and the proportion of weeks infested also support this hypothesis (Legendre, 1993). The similar behaviour of the proportion of weeks infested and total number of eggs was expected as the correlation observed between them was high.

Many authors support the proposition that *Ae. aegypti* oviposition can drive dispersal (Reiter *et al.*, 1995; Reiter, 1996; Edman & *et al.* 1998). The typical dispersion of *Ae. aegypti* is ~50–100 m, with maximums above 400–800 m (Morlan &

Hayes, 1958; Trpis *et al.*, 1995; Edman *et al.*, 1998; Muir & Kay, 1998; Honorio *et al.*, 2003). Recently, spatial structure of *Ae. aegypti* adults was detected in Iquitos, Peru; they clustered strongly at 10-m distances and weakly up to 30 m (Getis *et al.*, 2003). If the proportion of weeks infested or the total number of eggs reflected dispersal, we would have expected to see autocorrelation of these variables at ovitrap separations lower than the typical dispersal distances. We found no spatial autocorrelation owing to oviposition with 850-m trap separation; the high nuggets obtained in all the response variograms suggest studies with smaller separations between traps. This might help differentiate whether the high nuggets are due to high variability of the response variables or due to spatial dependence taking place at smaller distances.

The value of ovitrap data to estimate differences in vector abundance between blocks or neighbourhoods has been

Table 1. Multiple regression models parameters (*b*) and standard errors (SE) The proportion of weeks infested (PI) and the proportion of weeks infested excluding non-infested sites (PIo) as a function of urbanization variables. Densities per 100 m²; distances in km. The generalized linear model used binomial error distribution and pseudo-likelihood dispersion parameter estimation. The equation for the model is $PI = e^{LP}/(1 + e^{LP})$ with $LP = \text{ordinate} + b_1x_1 + b_2x_2 + b_3x_3$. The maximum correlation between parameters was 0.18.

	<i>b</i> (SE)			<i>b</i> (SE)		
	PI	d.f.	PI*	PIo	d.f.	PIo*
Ordinate	-2.000 (0.160)†	1	-2.000 (0.166)	-1.876 (0.143)†	1	-1.876 (0.142)
Flat density	-1.125 (0.195)†	1	-1.125 (0.168)	-0.709 (0.189)†	1	-0.709 (0.153)
House density	+2.677 (0.490)†	1	+2.677 (0.494)	+1.797 (0.444)†	1	+1.797 (0.440)
Distance to industries	-1.074 (0.202)†	1	-1.074 (0.200)	-0.684 (0.188)†	1	-0.684 (0.180)
Dispersion parameter	2.32			1.83		
Residual deviance	644	275		335	190	
Null deviance	1081	278		458	193	

* Jack-knifed parameters; † $t_{\infty} > 2.576$ significant at 1%.

questioned; it can be more reliably used to describe seasonal variability in adult productivity (Focks, 2003). High container densities in the trap surroundings might dilute the number of eggs detected or the amount of weeks infested, making it possible to confound a highly productive area with plenty of containers with a low production area. Although we do not know the relationship between ovitrap data and adult abundance, we might expect that higher standing crops in the site surroundings will raise the probability of the trap detecting oviposition, provided that container densities are similar. In Buenos Aires, the ovitraps detected differences between two cemeteries with equal container densities but, whereas the percentage of breeding sites differed by a factor of 18, the percentage of infested weeks differed only by a factor of 2 (Vezzani *et al.*, 2004). We used the accumulated number of eggs and the proportion of infested weeks during the year of study to resume seasonal variation at a single site and smooth stochastic variability. Studies carried out in the city between 1998 and 2001 showed that the ovitraps were consistent enough to describe the infestation pattern in space and time. More than 75% of the areas did not show any change in the rate of infestation from 1 year to another and 64% maintained the same rate of infestation over the 3 years

(Carbajo *et al.*, 2004). Although we do not know the relationship between oviposition and adult abundance, the spatial pattern observed in the city may reflect abundance differences at this coarse scale.

The development of *Ae. aegypti* requires resting sites, oviposition sites, nectar and blood sources (Christophers, 1960; Clements, 1992). Different levels of urbanization might be associated with the availability of these resources or with continuity between patches with resources, and thus affect the spatial pattern of infestation.

Differences in resource availability have been found in other cities. In Mexico the availability of flowering plants was higher in the periphery of the city and was associated with higher sugar feeding, which can enhance *Ae. aegypti* survival and fecundity (Martinez-Ibarra *et al.*, 1997). In Buenos Aires an association between mosquito breeding and vegetation cover was observed in cemeteries (Vezzani *et al.*, 2001). We found no relation between oviposition activity and vegetation cover on an urban scale. We used a coarse grain (100 × 100-m block) that distinguished only large vegetated areas like parks and plazas; small vegetated areas like gardens were not discriminated and, as they can be important to the mosquito, a more detailed scale should

Table 2. Multiple regression models parameters (*b*) and standard errors (SE) Total number of eggs per site (TE) and log total number of eggs excluding non-infested sites (TEo) as a function of urbanization variables. Densities per 100 m²; distances in km. The generalized linear model used Poisson error distribution and pseudo-likelihood dispersion parameter estimation. The equation for the model is $TEo = e^{LP}$ with $LP = \text{ordinate} + b_1x_1 + b_2x_2 + b_3x_3 + b_4x_4$. The maximum correlation between parameters was 0.21.

	<i>b</i> (SE)			<i>b</i> (SE)		
	TE	d.f.	TE*	TEo	d.f.	TEo*
Ordinate	4.769 (0.222)†	1	4.769 (0.217)	1.402 (0.062)†	1	1.402 (0.065)
Flat density	-1.210 (0.316)†	1	-1.211 (0.229)	-0.276 (0.065)†	1	-0.276 (0.089)
House density	3.141 (0.667)†	1	3.141 (0.632)	0.945 (0.194)†	1	0.945 (0.176)
Distance to industries	-1.510 (0.321)†	1	-1.510 (0.276)	-0.274 (0.075)†	1	-0.274 (0.180)
Distance to avenues				0.356 (0.161)‡	1	0.356 (0.139)
Dispersion parameter	123.4			0.36		
Residual deviance	24425	275		84.7	190	
Null deviance	39178	278		116.5	193	

* Jack-knifed parameters; † $t_{\infty} > 2.576$ significant at 1%; ‡ marginal significance.

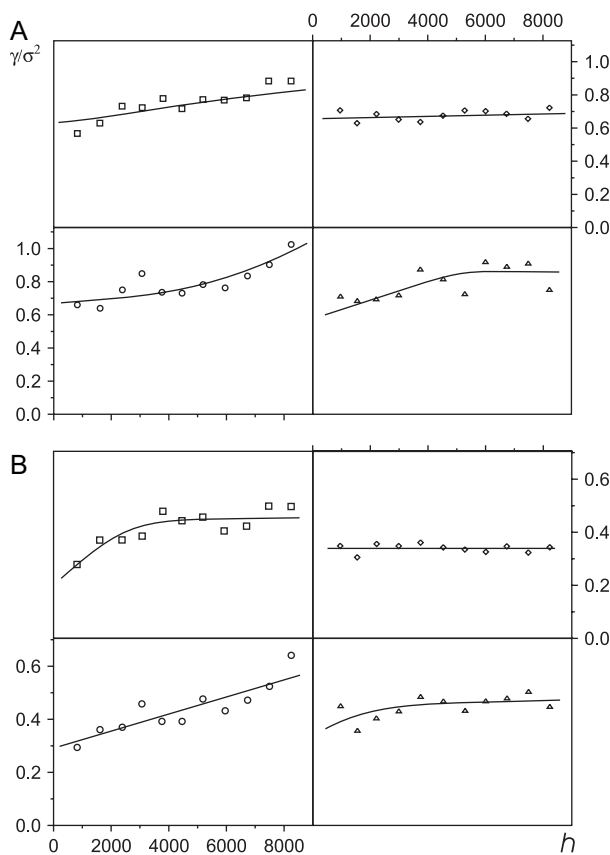


Fig. 5. Anisotropic standardized semivariograms of the GLM residuals for all sites. (A) Proportion of weeks infested, and (B) total number of eggs, both as a function of distance to industrial sites, flat density and house density. Directions of anisotropy are indicated by symbols: circles represent north–south (0°); triangles represent north–east–south–west (45°); squares represent east–west (90°), and rhombi represent north–west–south–east (135°). The ordinates show the standardized semivariance (γ/σ^2) and abscises the separation distance between points (h) in metres. Plotted semivariograms were fitted by weighted least squares.

be attempted. We found a positive association between ovitraps and industrial sites. Although water-filled containers were not studied, we would expect industrial sites to be related to higher container densities, and thus better breeding conditions. Blood sources for the mosquito may not be limited because the population density in Buenos Aires is high (150 inhabitants/hectare). We even found an inverse association of oviposition with population density. Probably the limiting resource is not blood, but vegetation or containers. Patches of vegetation are more commonly found in housing areas or in courtyards surrounded by multistorey buildings. It is possible that urbanization might be characterizing vegetation or container availability indirectly; for example, the proportion of built surface is lower in areas of high house density or low flat density and so the probability of finding resources outdoors may be higher.

A second explanation might be continuity because, in more highly populated areas, high-rise buildings are more frequent

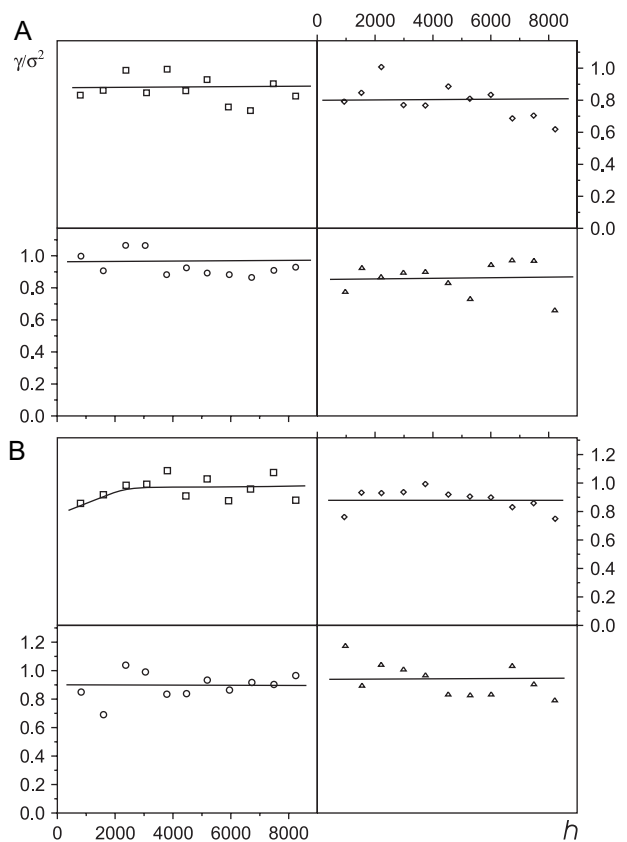


Fig. 6. Anisotropic standardized semivariograms of the GLM residuals for infested sites. (A) Proportion of weeks infested as a function of distance to industrial sites, flat density and house density. (B) Total number of eggs as a function of distance to industrial sites, flat density, house density and distance to avenues. Directions of anisotropy are indicated by symbols: circles represent north–south (0°); triangles represent north–east–south–west (45°); squares represent east–west (90°), and rhombi represent north–west–south–east (135°). The ordinates show the standardized semivariance (γ/σ^2) and abscises the separation distance between points (h) in metres. Plotted semivariograms were fitted by weighted least squares.

and can restrict free flight between the blocks or their courtyards, where breeding would be expected. The relationship with house and flat densities may also reflect this continuity conjecture. In Louisiana breeding sites were more frequent in vegetated shaded areas at the backs of houses or near the central courtyards of multistorey blocks (Focks *et al.*, 1981).

An additional possibility not related to resources might be that oviposition or development is affected by a heterogeneous spatial pattern of humidity or temperature. Fink *et al.* (1998) found that infestation was higher downtown. They postulated that the humidity generated by evaporative coolers may counteract desert conditions in the centre of town. In Buenos Aires relative humidity might not be restrictive to the vector as it fluctuates near 70%, but thermal heterogeneity might be important, given that Buenos Aires is close to the southern limit of *Ae. aegypti* distribution. Studies of heat island effects in the city showed that the downtown area can be warmer or colder depending on the

date, time of day and wind direction (Figuerola & Mazzeo, 1998; Leveratto *et al.*, 2000). A detailed spatio-temporal study of the relationship between temperature and oviposition is in progress.

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