Dispersal of *Aedes aegypti*: field study in temperate areas and statistical approach

Paula Bergero[1,+], Carlos A. Ruggerio[2], Ruben Lombardo[2,3], Nicolás Schweigmann[3], Hernán Solari[1]

[1]Departamento de Física FCEN-UBA and IFIBA-CONICET, [2]Área de Ecología, ICO-UNGS, [3]Departamento de Ecología, Genética y Evolución, FCEN-UBA

Financial Support: Universidad de Buenos Aires

[+] Corresponding Author: pbergero@df.uba.ar

We studied the dispersion of *Aedes aegypti* during egg laying in natural conditions. Two independent experiment involving mosquitoes dispersing from urbanization towards adjacent un-urbanized areas were carried out and analyzed in statistical terms. We find relations between stochastic variables related to the egg laying mosquito activity (ELMA), useful to asses dispersion probabilities, despite the lack of knowledge of the total number of ovipositions in the zone. We propose to evaluate the activity as minus the logarithm of the fraction of negative ovitraps at different distances from buildings. We also estimate the average number of eggs laid per oviposition using a regression between the ELMA and the number of eggs found. Three zones with different oviposition activity were determined, a corridor surrounding the urbanized area, a second region between 10m and 25m and the third region extending from 30m to 45m from the urbanization. The landscape (plant cover) and the human activity in the area appear to have an influence in the dispersal of *Aedes aegypti*.

Keyword index: *Aedes aegypti*, mosquitoes, dispersal, oviposition, multinomial analysis, dengue

INTRODUCTION

Ever since the identification by Finlay (Finlay 1886), and the confirmation by Reed (Reed et al. 1900), of *Aedes aegypti* as the vector of Yellow Fever the question: how far *Aedes aegypti* can fly, appears to be one of the most relevant questions (Boyce 1911, Shannon et al. 1930, Shannon & Davis 1930, Bugher & Taylor 1949, Wolfinsohn & Galun 1953), perhaps because of sanitary reasons such as anchoring vessels at a safe distance from the coast under quarentine conditions. In more recent times, the distance is useful for determining the area of comprehensive vector control in cases of Dengue infections (Honório et al. 2003, Russell et al. 2005).

In terms of the dispersion of *Aedes aegypti*, the interest shifts from: how far? into: how often can they be found at a given distance from their breeding sites or from human habitations? One of the earliest studies shows that under natural conditions *Aedes aegypti* preferred for oviposition places with natural shelter near by, but outside the habitations, and worked towards determining the distance from human housing at which this species may breed (Dunn 1927). Dispersion studies abound (Morlan & Hayes 1958, McDonald 1977, Trpis & Häusermann 1986, Trpis et al. 1995, Rodhain & Rosen 1997, Muir & Kay 1998, Ordoñez-Gonzalez et al. 2001, Getis et al. 2003, Harrington et al. 2005, de Freitas et al. 2007, de Freitas & de Oliveira 2009) yet there is high variability in the results reported that are in the range 20m (McDonald 1977) (experiment in a village in Kenya) to 2.5km (Wolfinsohn & Galun 1953) (experiment in the Sinai desert). Population models (Otero et al. 2008) as well as direct observations (Vezzani et al. 2004) indicate that dispersal is an important factor for the survival of *Aedes aegypti* in temperate urbane settings.

Several factors have been considered to explain the variability in the observed dispersion patterns. The lack of available oviposition places increases dispersion (Reiter et al. 1995, Edman et al. 1998), wind might decrease dispersion (Wolfinsohn & Galun 1953), environmental differences such as those resulting from different urbanization's (de Freitas et al. 2007, David et al. 2009) might exert an influence, while age of the released mosquitoes (in release-capture methods) is suggested as another influencing factor (Harrington et al. 2001).

The experimental method used appears to be an important factor as well. The methods used fall in two separated groups. A minority of studies correspond to natural dispersal (Dunn 1927, Rodhain & Rosen 1997), these studies indicate dispersion distances shorter than 200m (Dunn 1927) and 30-50m (Rodhain & Rosen 1997). The remaining works rely on the sequence breed-mark-release-capture mosquitoes using different marking methods and capturing either adults or eggs laid. We resume this information in the Appendix B. Release-capture methods appear as direct methods but the effects of the conditioning of the mosquitoes and the low number of recovered mosquitoes are a general concern. Furthermore, the release of a large number of mosquitoes vectors of dengue (and other diseases) imposes at times the need of further manipulation because of ethical concerns (Honório et al. 2003). Contrasting, using the local (natural) populations of *Aedes aegypti* appears as desirable but difficult to implement.

Moreover, beyond the intrinsic interest that represents for biology, the dispersal distance of *Aedes aegypti* is a highly relevant parameter in the mathematical modeling of the epidemiology of the diseases which it is a vector. The models are sensitive to both the type of dispersion (eg diffusion or directed flight) and the distances involved.

In this work we evaluate and discuss the dispersion of *Aedes aegypti* from building area towards seminatural adjacent areas. We develop and test a method, using egg-traps, that allow us to obtain estimates for the dispersal of *Aedes aegypti* in search of oviposition sites.

MATERIAL AND METHODS

Study area and sampling design

The studies were performed with ovitraps in two areas of the Province of Buenos Aires, Argentina. The climate is temperate, with rainfall over 1,000 mm per year, and 18 ºC annual average temperature.

One area was the Municipal Ecological Park, in Villa Elisa (VE), located at 34º51' S 58º4' W. It is a sylvan recreational park of 200 hectares characterized by steppe dominated by grasses, *Gleditsia triacanthos* (Honey locust) and Ligustrum (*Ligustrum sinence*). The inhabited environment around the park is semi rural. On the limit between the park and the adjacent residential houses 4 areas were selected, all considered auspicious to *Aedes aegypti*, but with differences in vegetation and shade. In the 4 zones of control, a total of 48 oviposition traps were distributed, on the edge of building surrounding houses. Two extra control ovitraps were placed close to the center of the park (at 600 to 1200 meters from the houses). Spread across the 4 areas of the park 130 ovitraps were arranged in a regular grid with 5 m spacing (3-4 columns, 8-12 rows), extending to a distance between 35 and 65 m off housing. Zones labelled as VE-1 and VE-2 had a street as an obstacle to dispersion (not monitored) and were both wooded. Zone VE-2 was next to a rest area following a footpath into the park. Zones VE-3 and 4 were crossed by a ditch (6m wide and 2m deep). Shadow was very scarce in zone VE-3 while VE-4 began with long grass and run into a dark forest. All VE zones were separated from each other several tens of meters.

The other area selected was a sector adjacent to a sub-officers neighborhood (Sargento Cabral) located in Campo de Mayo (CM), a military property of 5000 ha, at San Miguel county (34º32' S 58º39' W). Campo de Mayo is characterized by small residential areas, some military installations as well as wooded and crops areas, surrounded by an urbanization. The peridomiciliary area was considered as control zone. It is characterized by low houses with gardens partially wooded, where predominate grasses, shrubs and a variety of ornamental plants. In these gardens 53 ovitraps were placed under shrubs providing shade. Two sylvan contiguous zones, adjacent to the households, were chosen for the transects. The zone was delimited by a pre-existing fence that prevents access to people. The zones labelled as CM-1 and CM-2 present different characteristics. CM-1 is wooded dominated by Chinaberry (*Melia azedarach*), Ligustrum (*Ligustrum sinence*), Tala (*Celtis tala*) with sparse understory. CM-2 has a sector close to the households that is wooded (like zone CM-1) followed by a sector of grassland often flooded by rainwater, with scarce upland areas shaded by tallgrass. In the wild environment transects were drawn from households, equally spaced every 10 m: 4 transects in CM-1 and 4 in CM-2. In each transect 9 ovitraps were placed, spaced every 5 m and running into the field 10 to 55 m off the housing. In this case no extra control ovitraps where placed because the only nearby area in the park conducive to mosquito breeding is the “control area”.

Ovitrap monitoring was performed weekly during March-April 2010 (8 weeks). Oviposition was monitored using conventional black glass jar ovitraps. Each trap, with capacity of 330 ml, contained 100 ml of clean water and a 2x10 cm hardboard paddle resting against the upper rim. Cleaning and replacement of water and paddle was performed weekly. The paddles were examined under stereoscopic microscope (50X) and *Aedes aegypti* eggs were identified and counted.

At each study the control area and the grid of ovitraps running into the wild were distinguished. As control area we considered the homes and peri-domicile present on the edge of the urbanized area, *Aedes aegypti* dispersion measurements were made using transects of ovitraps perpendicular to the peri-domicile line bordering the park. The park was previously surveilled and the complete absence of containers (that could interfere with the experience) was assured.

Both areas of study are in the same climatic region -distant 67 Km one from the other-, located in the metropolitan area of Buenos Aires and the arrangement of transects was conducted in wilderness areas adjacent to low density residential areas. Also, in both experiments, we studied the border area of mosquito breeding areas. These conditions allowed to consider both experiments as replicas.

Dispersal activity

As a primary indicator for the dispersal of *Aedes aegypti* in natural conditions we considered the ``maximun distance'' where oviposition activity was detected at each area during the period covered by the experience. The landascape (plant cover and/or ditches or flooded grassland) and disturbance (as a percentage of ovitraps lost or damaged) was anotated as well.

Egg laying mosquito activity (ELMA)

The weekly activity for each area was evaluated as minus the logarithm of fraction of negative ovitraps at different distances in the transects and in the control area (see theory in the Appendix A). We evaluate ELMA as the number of ovipositions (*NO*) at a given distance with the statistics:

$$NO(x) \propto -\ln(1-\mathrm{p}(\mathrm{x})) \qquad (1)$$

where $p(x)$ is the fraction of positive ovitraps in the region characterized by x.

The spatial variation of oviposition (quality) activity was calculated as the relation between ELMA at the location and ELMA at the correspondig reference zone (control area).

As the insects go away from the source area (houses) we expected the preference for the ovitraps would decrease, and hence the quality (or attractiveness) of oviposition sites. The quality factor $\varepsilon(x)$ was calculated by

$$< NO(x) >= \varepsilon(x) < NO(c) > \qquad (2)$$

Where c indicates the control area and x is the distance from the urbanization in the grid, $<>$ indicate average values. The regresion offers an opportunity to monitor dispersion activity (see theory in the Appendix A)

The standard deviation of $\varepsilon(x)$ was calculated as:

$$|\,\varepsilon(x)-\varepsilon(x)^{*}\,| \approx \sqrt{\frac{\sum_i (NO(x)-\varepsilon(x)^{*}\,NO(x))^{2}}{(\sum_i NO(c))^{2}}} \qquad (3)$$

(see theory in the Appendix A). The estimation corresponds to the deviations from the linear relation conjectured weighted by the ELMA detected at the control zone.

Number Eggs per oviposition

The number of eggs present in each positive ovitrap was recorded. This number may be the result of a single or multiple ovipositions. Based on the number of eggs laid at each distance ($NE(x)$) and the activity in the same ovitraps the average number of eggs per ovipostion was calculated by the slope H of the regression (see theory in the Appendix A):

$$NE(x);\;\; H^{*}\,NO(x)+\zeta \qquad (4)$$

were ζ has zero mean. Notice that H^* is actually a random variable roughly independent of the activity

RESULTS

Dispersal activity

The maximum oviposition distances are shown in Table I for the different sets of transects (grids). In the areas without frequent human presence (VE-1, VE-3, VE-4, CM-1 and CM-2) ovipositions were detected up to 20 and 40m from the construction line, while in the most disturbed grid (VE-2) it was recorded al 65m, further away from the urbanization.

Table I: Environment and flight

Zone	Distance [m]	Plant cover	H-disturbance
VE-1	40	trees, long grass	1.5
VE-2	65	trees, short grass	22.4
VE-3	30	short grass, ditch, long grass	5.8
VE-4	40	long grass, ditch, forest	5.1
CM-1	40	trees	2,4
CM-2	20	trees followed by flooded grassland	2,4

Environmental details and maximum distances for *Aedes aegypti*. VE: Villa Elisa experiment, CM: Campo de Mayo experiment, H-disturbance= percentage of ovitraps lost.

In CM no ELMA was detected at the grassland sector nor at the tallgrass shaded areas. All the egg laying activity corresponded to the wooded area both in CM-1 and CM-2, including a single ovitrap in an isolated wooded patch within the grassland area. In the wooded environment with continuous tree cover (CM-1), there was preference for oviposition in areas with higher density of understory and ground vegetation, but up to a maximum distance of 40m. There were no oviposition at greater distances despite maintaining the structure of vegetation.

Egg laying activity in the control areas

The ELMA detected at the different control areas fluctuated with every weekly inspection. The fluctuations had a local character and the four zones in VE do not present the same patterns despite being in geographic proximity, (Figure 1). In the 2 ovitraps placed at the center of the park (VE experiment) no ELMA was detected.

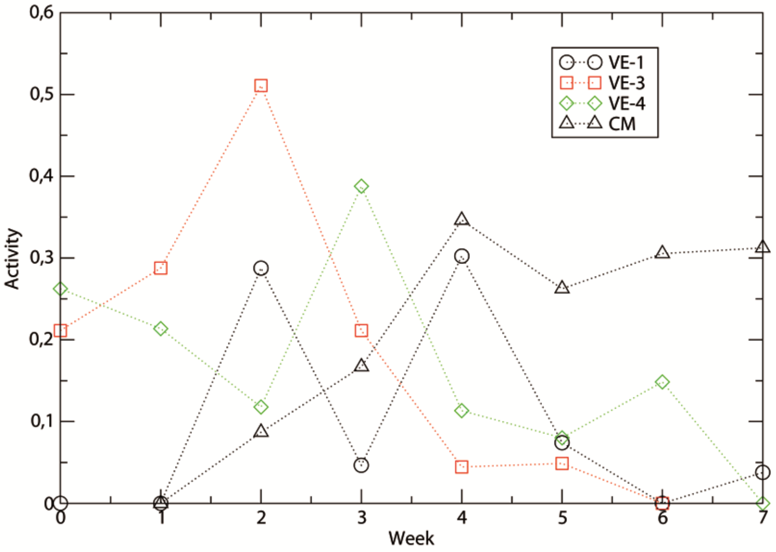

Figure 1: Oviposition activity at the reference zones of the undisturbed grids as a function of time for the transects VE-1, VE-3, VE-4 and CM.

Egg laying activity in the grids

Using equation ((2)) of the conceptual probabilistic model developed we computed the quality (preference) factor as it changes with the distance to the urbanization. We found 3 dispersal levels: 0-10m, 10-25m, and 30-40m (distances are referred to the construction line). See Figure 2.

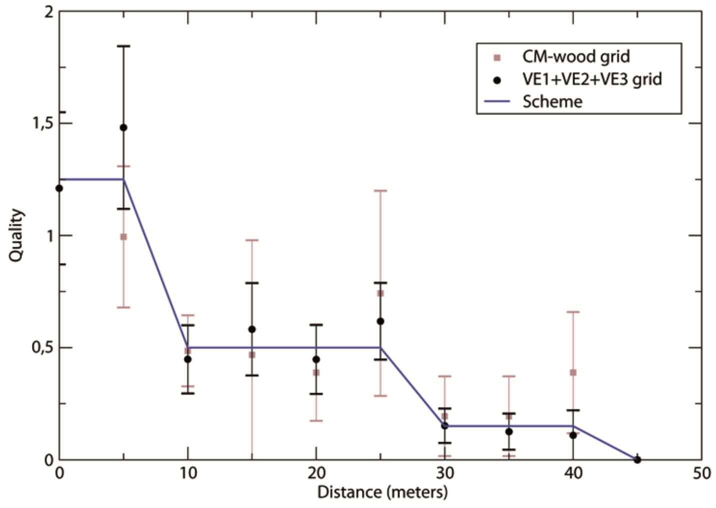

Figure 2: Relative activity as a function of the distance to the construction line (control zone) collecting observations in undisturbed VE zones and wooded areas in CM-1 and CM-2. Error bars correspond to the standard deviation.

In both experiments we observed that the tree cover favors the dispersal of *Aedes aegypti*. Additionally, we observe that the ditch in VE-3 and VE-4 (4m wide, 2m deep) is not an insurmountable obstacle.

Number of eggs per oviposition

The dispersal of eggs responds to two factors, ELMA and the number of eggs oviposited (in average) per oviposition. On this second factor, the estimate of the average number of eggs laid per oviposition by the average female are shown in Table II.

Table II: Eggs per oviposition

Distance [m]	**Villa Elisa**			**Campo de Mayo**		
	*H**	*SD(H)*	*D(H*)*	*H**	*SD(H)*	*D(H*)*
Control Area	18.1	8.6	3.1	14.6	2.8	1.6
0-5	12.0	9.9	2.6	12.5	5.1	3.0
10-25	13.3	9.2	2.6	8.7	5.0	1.9
30-45	13,4	6.4	4.5	9.1	2.5	2.3
Total Grid (0-40)	12.7	9.4	1.8	12.3	2.0	2.3

Estimated number of eggs per oviposition in the control areas, the 3 dispersal levels detected and the total grid at VE and CM. Average number of eggs per oviposition, $H*$, standard deviation per estimation, $SD(H)$, and standard deviation of the mean, *SD(H*)*.

While the statistics gathered is not completely conclusive, the difference in the average number of eggs laid when ovipositing in VE corresponds to $P(|x| \geq ((18.1-12.7)/3.6) < 0.14$ (assuming a normal distribution for the difference between means). The difference in CM is not significant (P<0.41). Also, the Figure 3 show the cumulative frequency of the number of eggs found in the ovitraps for both areas (VE and CM).

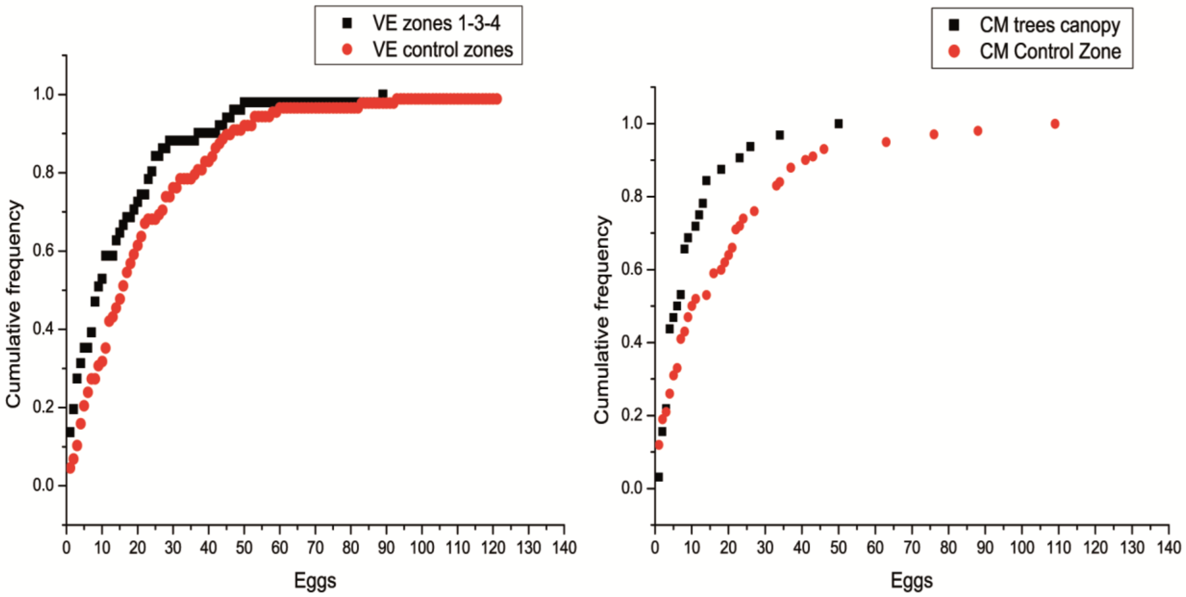

Figure 3: Cumulative frequency of the number of eggs found in the ovitraps for VE (left) and CM (right). Control zones are represented by circles and transects by squares.

We illustrate the regressions in the control areas of VE in Figure 4.

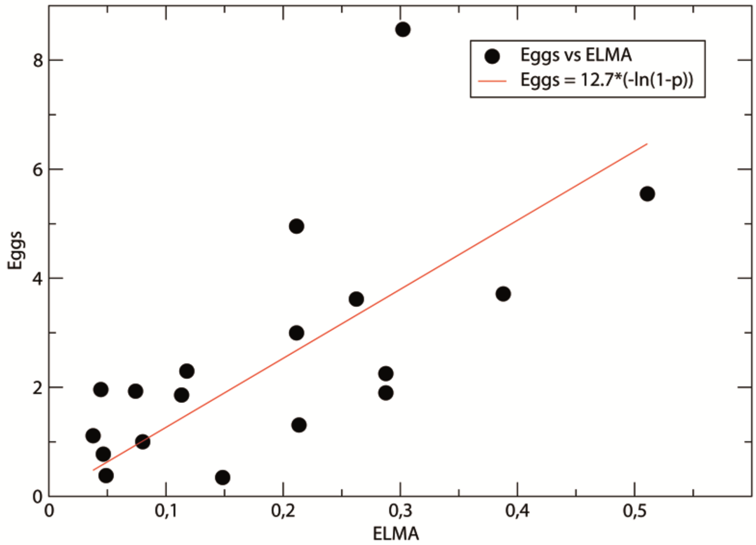

Figure 4: The terms of the regression and estimated number of eggs laid in a single oviposition for the grids in VE1, VE3, VE4. Y axis: average number of eggs detected in positive ovitraps, X axis: minus logarithm of fraction of negative ovitraps.

DISCUSSION

The present results are consistent between the two independent replicates performed as well as with previous results using natural methods (Dunn 1927, Rodhain & Rosen 1997), a fact that by contrast suggests that mark-release-capture experiments exaggerate the dispersion pattern and depend on uncontrolled variables.

Our results indicate that *Aedes aegypti* explores the area surrounding its breading sites searching for oviposition sites. The ELMA decreases with the distance to the building line. Between five and ten meters away ELMA drops to a half of the activity in the reference, urban, zone. About thirty meters away from the houses the ELMA is a quarter of the activity in the reference zone and we detected no activity in undisturbed zones further away than 40m. These results suggest that the dispersion distances for *Aedes aegypti* are short, in agree with Getis et al (Getis et al. 2003), but differ in this sense from measurements made with previously manipulated mosquitoes (Reiter et al. 1995, Honório et al. 2003).

The dispersion of eggs however seems to be lower than oviposition as dispersing females tend to lay a lower number of eggs in average, relative to those in the control (source) area. The difference detected between CM and VE may indicate a real difference in terms of behavior since it correlates with the fact that the activity in CM was rising when the activity in VE was falling (Figure 1). The relative isolation of the “Barrio de Suboficiales Sargento Cabral” with respect to the larger urbanization in the county contrasts with the study area in VE that belongs to a much larger continuous urbanization. This suggest that we are in fact observing mosquito behavioral characteristics, that are robust in front of different enviromental situations. The possibility of *Aedes aegypti* reaching CM facilities as a result of their summer dispersion cannot be ruled out.

The landscape has an impact in the dispersion pattern (Russell et al. 2005, de Freitas & de Oliveira 2009). In this work, wood plant cover appears to facilitate dispersion and create corridors for the mosquito, see Table **¡Error! No se encuentra el origen de la referencia.**. The results suggest that human activity facilitates short range dispersion as well. In contrast, the monticules shaded by tallgrass in the often flooded grassland are avoided by *Aedes aegypti*. This suggests that for control situations the degree of environmental favorability (quality) and anthropic disturbance of the target area should be considered.

The method of measurement proposed has several advantages and some obvious inconvenience’s. Main advantages: it does not introduce new vectors to the area, but rather it eliminates a few them in the form of eggs; the initial conditions of the experiment are not singular and, thus, several factors have not necessary been included in the analysis. Factors such as place chosen for the release, time and weather conditions at the release and subsequent days, age profile of the mosquitoes released, influence of density dependent effects such as egg laying inhibition (Chadee 2009), influence of the preparation of the mosquitoes (breeding, marking, ...). In contrast, the main difficulty is not knowing the number of mosquitoes that lay eggs in the zone being studied during the collection time, a second problem is the observed influence of human movements in the dispersion of *Aedes aegypti*, although this is a problem out of the virtue of being able to detect such an influence. Furthermore, the mosquito population fluctuates with temperature and would be expected that fluctuations in nearby areas are coordinated, nevertheless the activity in VE zones shows low correlation, which complicates the statistics.

The method gives consistent results between independent realizations of the experiment. It allows to explore questions such as the influence of breeding sites availability on dispersion.

The lack of knowledge of the total number of ovipositions in the zone and period considered is not an impediment to the statistical analysis performed since the unknown variable occurs in the same form in the control zone and in the transects, thus allowing for meaningful comparisons between them.

Low repetition numbers have been an obstacle to the present research particularly because of the variability of the ELMA at different zones and times. The method developed allowed to use the data gathered in a consistent form, beyond naive approximations.

Aedes aegypti activity was detected up to 40m away from the peri-domicile, its activity decreases as the distance to the urbanization decreases. A small zone, up to 5m in the grids, presents an activity comparable to the control area (1.25 realtive activity), decreasing to 0.5 in the 10-25m zone, and further decreasing to 0.15 at the 30-40m zone. No oviposition was detected beyond this distance in the grids not disturbed by human activity. When human activity was present, the maximun distance detected was of 65m, suggesting that human presence influences the dispersion. Plant cover was a determining factor for dispersion, its absence appears to deterre it (grassland with scarce tallgrass) while the presence of woods makes a sort of corridor for dispersion.

We suggest as well that the egg laying behaviour (eggs laid per oviposition) could be different at the grids (sylvan zone) and the control areas (urban zone), but this results require, for confirmation, a repetition of the experiment gathering more statistical samples.

REFERENCES

Boyce R 1911. Yellow fever and its prevention. EP Dutton and Co, New York.

Bugher JC, Taylor M 1949. Radiophosphorus and radiostrontium in mosquitoes. preliminary report. *Science 110:*146–147.

Chadee DD Sep 2009. Oviposition strategies adopted by gravid *Aedes aegypti* (l.) (diptera: Culicidae) as detected by ovitraps in trinidad, west indies (2002-2006). *Acta Trop 111 3:*279–283*. Available from:* http://dx.doi.org/10.1016/j.actatropica.2009.05.012

Christophers R 1960. *Aedes aegypti* (L.), the yellow fever mosquito. Cambridge Univ. Press., Cambridge.

David MR, de Oliveira RL, de Freitas RM 2009. Container productivity, daily survival rates and dispersal of aedes aegypti mosquitoes in a high income dengue epidemic neighbourhood of rio de janeiro: presumed influence of differential urban structure on mosquito biology. *Mem Inst Oswaldo Cruz 104(6):*927–932*.*

de Freitas RM, Codeço CT, de Oliveira RL 2007. Daily survival rates and dispersal of *Aedes aegypti* females in rio de janeiro, brazil. *Am J Trop Med Hyg 76(4):*659–665*.*

de Freitas RM, de Oliveira RL 2009. Presumed unconstrained dispersal of *Aedes aegypti* in the city of rio de janeiro, brazil. *Rev Saude Publica 43(1):8–12.*

Dunn LH 1927. Observations on the oviposition of *Aedes aegypti* linn., in relation to distance from habitations. *Bull Ent Res 18:*145–148*.*

Edman JD, Scott TW, Costero A, Morrison AC, Harrington LC, Clark GG 1998. *Aedes aegypti* (diptera culicidae) movement influenced by availability of oviposition sites. *J Med Entomol 35(4):*578–583*.*

Finlay C 1886. Yellow fever: Its transmission by means of the culex mosquito. *Am J Med Sci 184:*395–408.

Getis A, Morrison AC, Gray K, Scott TW 2003. Characteristics of the spatial pattern of the dengue vector, *aedes aegypti*, in iquitos, peru. *Am J Trop Med Hyg 69(5):*494–505.

Harrington LC, Buonaccorsi JP, Edman JD, Costero A, Kittayapong P, Clark GG, Scott TW 2001. Analysis of survival of young and old *Aedes aegypti* (diptera: Culicidac) from puerto rico and thailand. *J Med Entomol 38(4):*537–547.

Harrington LC, Scott TW, Lerdthusnee K, Coleman RC, Costero A, Clark GG, Jones JJ, Kitthawee S, Kittayapong P, Sithiprasasna R, Edman JD 2005. Dispersal of the dengue vector *Aedes aegypti* within and between rural communities. *Am J Trop Med Hyg 72(2):*209–220.

Honório NA, da Costa Silva W, Leite PJ, Gonçalvez JM, Lounibos LP, de Oliveira RL 2003. Dispersal of *Aedes Aegipty* and *Aedes Albopictus* (dipetera culicidae) in an urban endemic dengue area in the state of rio de janeiro, brasil. *Mem Inst Oswaldo Cruz 98:*191–198.

McDonald PT 1977. Population characteristics of domestic *Aedes aegypti* (diptera: Culicidae) in villages on the kenya coast. ii. dispersal within and between villages. *J Med Entomol 14(1):*49–53.

Morlan HB, Hayes RO 1958. Urban dispersal and activity of *Aedes aegypti*. *Mosq News 18:*137–144.

Muir LE, Kay BH 1998. *Aedes aegypti* survival and dispersal estimated by mark-release-recapture in northern australia. *Am J Trop Med Hyg 58:*277–282.

Ordoñez-Gonzalez JG, Mercado-Hernandez R, Flores-Suarez AE, Fernandez-Salas I 2001. The use of sticky ovitraps to estimate dispersal of *Aedes aegypti* in northeastern mexico. *J Am Mosq Control Assoc 17(2)*:93–97.

Otero M, Schweigmann N, Solari HG 2008. A stochastic spatial dynamical model for *Aedes aegypti*. *Bull Math Biol 70:*1297–1325.

Reed W, Carroll J, Agramonte A, Lazear JW 1900. The etiology of yellow fever - a preliminary note. *Public Health Pap Rep 26:*37–53.

Reiter P, Amador MA, Anderson RA, Clark GG 1995. Short report: Dispersal of *Aedes aegypti* in an urban area after blood feeding as demonstrated by rubidium-marked eggs. *Am J Trop Med Hyg 52:*177–179.

Rodhain F, Rosen L 1997. Mosquito vectors and dengue virus-vector relationships. In: Gubler DJ, Kuno G (Eds.), Dengue and Dengue Hemorrhagic Fever. CAB International, New York, pp. 61–88.

Russell RC, Webb CE, Williams CR, Ritchie SA 2005. Mark-release-recapture study to measure dispersal of the mosquito *Aedes aegypti* in cairns, queensland, australia. *Med Vet Entomol 19:*451–457.

Shannon RC, Burke AW, Davis NC 1930. Observations on released stegomyia aegypti (l.) with special reference to dispersion. *Am J Trop Med 10:*145–150.

Shannon RC, Davis NC 1930. The flight of stegomyia aegypti (l). *Am J Trop Med 10:*151–156.

Trpis M, Hausermann W, Jr GBC 1995. Estimates of population size, dispersal, and longevity of domestic *Aedes aegypti* (diptera: Culicidae) by mark-release-recapture in the village of shauri moyo in eastern kenya. *J Med Entomol 32:*27–33.

Trpis M, Hausermann W 1986. Dispersal and other population parameters of *Aedes aegypti* in an african village and their possible significance in epidemiology of vector-borne-diseases. *Am J Trop Med Hyg 35:*1263–1279.

Vezzani C, Velázquez ST, Schweigmann N 2004. Seasonal pattern of abundance of *Aedes aegypti* (diptera: Culicidae) in Buenos Aires city, argentina. *Mem Instit Oswaldo Cruz 99:*351–356.

Wiseman RH, Symes LB, McMahon JC, Teesdale C 1939. Report on a malaria survey of Mombasa. *Nairobi Goverment Printer, Nairobi.*

Wolfinsohn M, Galun R 1953. A method for determining the flight range of *Aedes aegypti* (linn.). *Bull Res Council Israel 2:*433–436.

APPENDICES

Appendix A: Multinomial theory for egg laying

Ovitrap positivity

In this section we seek to find relations between stochastic variables related to egg laying mosquito activity, ELMA, to be used to asses dispersion probabilities. We will consider as a first approximation that at every oviposition an individual mosquito has a choice between K_{BS} breeding sites which can be located by the mosquito with a relative weight of 1, K_C ovitraps in the control zone with same relative weight that breeding sites (this relative weight plays in fact no other role than lightening the notation), and K_x ovitraps at a sampled distance x which can be located with a relative weight $\varepsilon(x)$ that we will name the quality of the ovitrap and is the target of our investigation. The quality indicates the relative preference for an ovitrap at a distance x with respect to those in the control area. Let N be

$$N = K_{BS} + K_C + \sum_x (K_x \varepsilon(x)) \tag{5}$$

the effective total number of options for egg laying (K indicates number and the subscripts stand for breeding sites, BS, control, C, and value of distance, x and let

$$p_{BS} = \frac{1}{N} \tag{6}$$

$$p_C = p_{BS} \tag{7}$$

$$p_x = \varepsilon(x)/N \tag{8}$$

be the probabilities of oviposition corresponding to a breeding site, an ovitrap in the control area, and an ovitrap at a distance x respectively. Then, the probability for an ovitrap located at x to be negative (meaning have no eggs trapped) after NO ovipositions is:

$$p_{neg}(x) = 1 - p_{POS}(x) = (1 - \varepsilon(x)/N)^{NO} \tag{9}$$

which can be approximated for N large as

$$p_{neg}(x) = \exp(-\varepsilon(x) NO/N) \tag{10}$$

with $\varepsilon(BS) = 1 = \varepsilon(C)$. Thus, we obtain the basic result that for fixed N, $-\ln(p_{neg}(x))$ is roughly proportional to the random number NO that represents the total number of ovipositions in the period, being the proportionality factor $\varepsilon(x)/N$ the quality of ovitraps divided by the (unknown) number of effective oviposition sites available, as such $-\ln(p_{neg}(x))$ is a measure of ELMA. The regression

$$-\ln(\hat{p}_{neg}(x));\ -A\ln(\hat{p}_{neg}(C)) \tag{11}$$

(where $\hat{p}$ is a random estimate of p) allows to estimate the quality factor $\varepsilon(x)$ using the slope of the regression (11). We thus obtain

$$A=\varepsilon(x)=<\ln(\hat{p}_{neg}(x))>/<\ln(\hat{p}_{neg}(C))> \tag{12}$$

by the law of large numbers ($<>$ indicate average values) and offers an opportunity to monitor dispersion activity.

Egg numbers

Since *Aedes aegypti* lays its eggs in several ovipositions at the end of each gonotrophic cycle chri60,chad09, the number of eggs laid in a zone x, $NE(x)$, is

$$NE(x)=\sum_{j=1} jn_j(x) \tag{13}$$

where n_j (x) is the number of ovipositions of precisely j eggs. The total number of ovipositions at x is $NO(x)=\sum_j n_j(x)$, and then if we define $H=<NE(x)>/<NO(x)>$ the average number of eggs per oviposition in the zone x. The slope of the regresion

$$NE(x);\ H\,NO(x)+\zeta \tag{14}$$

allows us to estimate H (here ζ stands for a fluctuation with zero mean).

Error estimates

The expression (14) allows to estimate the average number of eggs per oviposition. Consider for example estimating H in (14) from a series of pairs

$$(\alpha_{i,}\beta_i)=(-\ln(p_{neg}),ne)_i\ i=1\ldots M \tag{15}$$

as

$$H=\frac{\sum_i \beta_i}{\sum_i \alpha_i} \tag{16}$$

Where ne_i are the number of eggs per positive ovitrap. The correct relation is

$$H^*=\frac{<\beta>}{<\alpha>} \tag{17}$$

then

$$\psi_i = (\alpha_i H^* - \beta_i) \qquad (18)$$

are N variables with zero average and subject to the relation ((16)), but otherwise independent.

$$\psi_i + (H - H^*)\alpha_i \qquad (19)$$

then

$$< (\sum_i \psi_i)^2 >= (H - H^*)^2 < (\sum_i \alpha_i)^2 > \qquad (20)$$

and we estimate the characteristic error as

$$| H - H^* | : \sqrt{\frac{\sum_i \psi_i^2}{(\sum_i \alpha_i)^2}} \qquad (21)$$

Notice that the latter relation uses the independence of each estimation and that $< \psi_i >= 0$

The same technique can be used to obtain error estimates for $\varepsilon(x)$, the quality factors.

Appendix B: Dispersion experiments, a summary

Dispersion studies of *Aedes aegypti-Part I*.

Reference	Environment	Method	Released	Recovered (%)	Time (day)	MD (m)	MDT/ range	Comments
Boyce 1911	-	observation	-	-		-	50-100 yards	Bouffard: MD=100 m; Le Moal: MD=250 m
Dunn 1927	periurban-Nigeria	natural conditions/ larvae collection	-	-		457	-	preference for ovipositing outside of houses (with bushes and trees)
Shannon et al. 1930	urban-Brazil	release/capture	3500	5.3-69.5	2-17	120	-	-
Shannon & Davis 1930	urban/boat-Brazil	release/capture	34350	0.4	2-5	1000*	-	4 releases, 1 from a boat*
Wiseman et al. 1939	Nairobi	release/capture					732*	exp. to verify if was possible for the island to be invaded from the mainland *crossing water
Bugher & Taylor 1949	Nigeria	release/capture	276221	0.1	-	1158	-	4 experiments, radioactive mosquitoes 9-28 days old
Wolfinsohn & Galun 1953	desert-Israel	release/ovitraps	73000	-	1	2500	-	2 experiments, in absence of wind the dispersal was greater
Morlan & Hayes 1958	urban-USA	release/capture	9215	4.7	1	175	-	10 experiments
McDonald 1977	village-Kenya	release/capture	720/10743 *	38/10-59*/	12	800*	-	Intravillage dispersal: 20 m. Intervillage dispersal*: 200 m
Trpis & Häusermann 1986	village-Kenya	release/multiple capture	824	40	1	154/113	57/44.2	recaptures up to 10 times, differences for male/female
Reiter et al. 1995	urban-Puerto Rico	release/ovitraps	90	-	5	420	-	flight in urban area is oviposite-driven

MD: maximum displacement, MDT: mean distance traveled.

Dispersion studies of *Aedes aegypti-Part II*.

Reference	**Environment**	**Method**	**Released**	**Recovered** (%)	**Time** (day)	**MD** (m)	**MDT/** range	**Comments**
Trpis et al. 1995	village-Kenya	release/capture	2000	17	9	120	49 (1 day)	MDT: 51,4 m in 2 days, 63,6 m in 3 days, mosquitoes reached all houses within 24 hs of release
Rodhain & Rosen 1997	-	-	natural conditions			1	30-50	females rarely visit more than 2 or 3 houses in their lifespan
Muir & Kay 1998	rural-Australia	release/capture	68	3.6-13	7	160	35/56	different MDT for male/female
Ordoñez-Gonzalez et al. 2001	urban-Mexico	release/capture	401	7.7	1-19	120	30.5	4 linear transects of sticky ovitraps in an area of 300 m in diameter
Getis et al. 2003	urban in Amazon forest-Peru	aspiration collections	-	-	1	-	0-30	clustering analysis
Honório et al. 2003	urban-Brazil	release/ovitraps	3055	-	6	800	-	proboscis amputation
Harrington et al. 2005	urban-Thailand, Puerto Rico	release/capture	11355	4-34	4-12	566	31-199	21 experiments in 11 years
Russell et al. 2005	suburban-Australia	release/capture	1948	3.4	11	175	78	environmental factors affect direction
de Freitas et al. 2007	suburban, slum-Brazil	release/capture	8792	6.8-14.3	8-13	363	40-87	dispersal higher in suburban area
de Freitas & de Oliveira 2009	urban-Brazil	release/capture	725	6.3	2-9	690	288.12	no evidence of a preferred direction
David et al. 2009	urban, suburban, slum-Brazil	release/capture	1750	5-12.2	1-10	263	57-122	urban structure can influence mosquito biology

MD: maximum displacement, MDT: mean distance traveled.