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Research Articles

Dispersal of *Aedes aegypti:* Field study in temperate areas using a novel method

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ABSTRACT

Background & objectives: Since *Aedes aegypti* was identified as vector of yellow fever and dengue, its dispersal is relevant for disease control. We studied the dispersal of *Ae. aegypti* in temperate areas of Argentina during egg-laying, using the existing population and egg traps.

Methods: Two independent replicas of a unique experimental design involving mosquitoes dispersing from an urbanized area to adjacent non-urbanized locations were carried out and analyzed in statistical terms.

Results: We found relationship between stochastic variables related to the egg-laying mosquito activity (ELMA), useful to assess dispersal probabilities, despite the lack of knowledge of the total number of ovipositions in the zone. We propose to evaluate the egg-laying activity as minus the logarithm of the fraction of negative ovitraps at different distances from the buildings.

Interpretation & conclusion: Three zones with different oviposition activity were determined, a corridor surrounding the urbanization, a second region between 10 and 25 m and the third region extending from 30 to 45 m from the urbanization. The landscape (plant cover) and the human activity in the area appear to have an influence in the dispersal of *Ae. aegypti*. The proposed method worked consistently in two different replicas.

Key words *Aedes aegypti;* dengue; dispersal; multinomial analysis; oviposition; yellow fever

INTRODUCTION

Ever since the identification by Finlay[1], and the confirmation by Reed *et al*[2], of *Aedes aegypti* as the vector of yellow fever the question: How far *Ae. aegypti* can fly, has been one of the most relevant questions[3–7], perhaps because of sanitary reasons such as anchoring vessels at a safe distance from the coast under quarantine conditions. In more recent times, the distance is useful for determining the area of comprehensive vector control in cases of dengue infections[8–9].

In terms of the dispersal of *Ae. 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 *Ae. aegypti* prefer to lay eggs in places with natural shelter nearby, but outside the habitations, and worked towards determining the distance from human housing at which this species may breed[10]. Several studies on dispersal of this species have been conducted[11–21], indicating high variability in the range of 20 m[12] to 1 km[6].

Population models[22] as well as direct observations[23] indicate that dispersal is an important factor for the survival of *Ae. aegypti* in temperate urban settings. Several factors have been considered to explain the variability in the observed dispersal patterns. The lack of available oviposition places increases dispersal[24–25], wind might decrease dispersal[7], and environmental differences such as those resulting from different urbanizations might exert an influence[20–26], while age of the released mosquitoes (in release-capture methods) is suggested as another influencing factor[27].

The experimental method used appears to be an important factor as well. In this work, we will refer to natural dispersal when measurements are made using the pre-existing local population and with a minimal intervention in the environment, contrasting with the dispersal measured under (singular, adhoc) experimentally created situations.

Table 1. Dispersal studies of *Aedes aegypti*

Reference	Environment	Method	Released	Recovered (%)	Time (Day)	MD (m)	MDT/ Range	Comments
Boyce[3]	–	Observation	–	–		–	50–100 yards	Bouffard: MD = 100 m; Le Moal: MD = 250 m
Dunn[10]	Periurban-Nigeria	Natural conditions/ larvae collection	–	–		457	–	Preference for ovipositing outside of houses (with bushes and trees)
Shannon *et al*[4]	Urban-Brazil	Release/capture	3500	5.3–69.5	2–17	120	–	–
Shannon & Davis[5]	Urban/boat-Brazil	Release/capture	34350	0.4	2–5	1000*	–	Four releases
Wiseman *et al*[28]	Nairobi	Release/capture					732†	Experiments to verify, if it was possible for the island to be invaded from the mainland
Bugher & Taylor[6]	Nigeria	Release/capture	276221	0.1	–	1158	–	Four experiments, radioactive mosquitoes 9–28 days old
Wolfinsohn & Galun[7]	Desert-Israel	Release/ovitraps	73000	–	1	2500	–	Two experiments, in the absence of wind the dispersal was greater
Morlan & Hayes[11]	Urban-USA	Release/capture	9215	4.7	1	175	–	Ten experiments
McDonald[12]	Village-Kenya	Release/capture	720/10743‡	38/10–59‡	12	800‡	–	Intervillage dispersal: 20 m. Intervillage dispersal: 200 m
Trpis & Häusermann[13]	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*[24]	Urban-Puerto Rico	Release/ovitraps	90	–	5	420	–	Flight in urban area is oviposit driven
Trpis *et al*[14]	Village-Kenya	Release/capture	2000	17	9	120	49 (1 day)	MDT: 51, 4 m in two days, 63, 6 m in three days, mosquitoes reached in all the houses within 24 h of release
Rodhain & Rosen[15]	–	Natural conditions			1		30–50	Females rarely visit >2 or 3 houses in their life span
Muir & Kay[16]	Rural-Australia	Release/capture	68	3.6–13	7	160	35/56	Different MDT for male/ female
Ordoñez-Gonzalez *et al*[17]	Urban-Mexico	Release/capture	401	7.7	1–19	120	30.5	Four linear transects of ovitraps in an area of 300 m in diam
Getis *et al*[18]	Urban in Amazon forest-Peru	Aspiration collections	–	–	1	–	0–30	Clustering analysis
Honório *et al* [8]	Urban-Brazil	Release/ovitraps	3055	–	6	800	–	Proboscis amputation
Harrington *et al*[19]	Urban-Thailand, Puerto Rico	Release/capture	11355	4–34	4–12	566	31–199	21 experiments in 11 years
Russell *et al*[9]	Suburban-Australia	Release/capture	1948	3.4	11	175	78	Environmental factors affect direction
de Freitas *et al* [20]	Suburban, slum-Brazil	Release/capture	8792	6.8–14.3	8–13	363	40–87	Dispersal higher in suburban area
de Freitas & de Oliveira[21]	Urban-Brazil	Release/capture	725	6.3	2–9	690	288.12	No evidence of a preferred direction
David *et al*[26]	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 travelled; *From a boat; †Crossing water; ‡Inter village dispersal.

In the case of *Ae. aegypti* dispersal, a few of the studies correspond to natural dispersal; these studies indicate dispersal distances shorter than 200 m[10] and 30–50 m[15]. The remaining works rely on the sequence breed-mark-release-capture mosquitoes using different marking methods and capturing either adults or eggs laid. We summarize this information in Table 1. Release-capture methods appear as direct methods but the effects of the conditioning of the mosquitoes and the low number of recovered mosquitoes are of concern.

Furthermore, the release of numerous mosquito vectors of dengue and other diseases imposes at times the need of further manipulation because of ethical concerns[8]. In contrast, using the local (natural) populations of *Ae. aegypti* appears as desirable but difficult to implement. Moreover, beyond the intrinsic interest that represents biology, the dispersal distance of *Ae. aegypti* is a highly relevant parameter in the mathematical modeling of *Ae. aegypti*-borne disease epidemiology.

In this work, we evaluate and discuss the dispersal of *Ae. aegypti* from housing area towards semi-natural (non-urbanized, with wild vegetation growing freely) adjacent area. We developed and tested a method, using egg-traps (here after ovitraps), that allowed us to obtain estimates for the dispersal of *Ae. aegypti* in search of oviposition sites.

MATERIAL & METHODS

Study design

In order to evaluate mosquito dispersal during egg-laying we seek opportunities in the limits between extended urbanized and non-urbanized ("wild") areas. The contrast between an area that offers breeding sites and opportunities for blood meals with an area lacking both conditions allows us to assume that the core of the home range of the mosquito is the urbanized area and therefore, investigate their dispersal by detecting the presence of *Ae. aegypti* in the wild zone as a function of the distance to border of the urbanization.

We detect the presence of mosquitoes by monitoring their egg-laying activity (ELMA) using ovitraps. We seek to quantify mosquito dispersal comparing the activity detected in the core of their home range (hereafter reference zone) and its decline moving into the adjacent wild area as a function of the distance to the border of the urbanization.

We consider that in each opportunity a mosquito lays eggs as it has a choice between the existing breeding sites, the ovitraps in the reference zone and the ovitraps at various distances going into the wild area, and propose to use the positivity of the ovitraps (i.e. the fraction between ovitraps presenting eggs and the total number of ovitraps with similar locations) as a method for quantitatively assessing the dispersal of the mosquitoes.

Study sites

The studies were performed with ovitraps in two locations of the Province of Buenos Aires, Argentina (Fig. 1). The climate is temperate with the average annual temperature of 18°C and rainfall exceeds 1000 mm per year. One location was the Parque Ecológico Municipal, in Villa Elisa (VE), located at 34º 51' S and 58º 4' W.

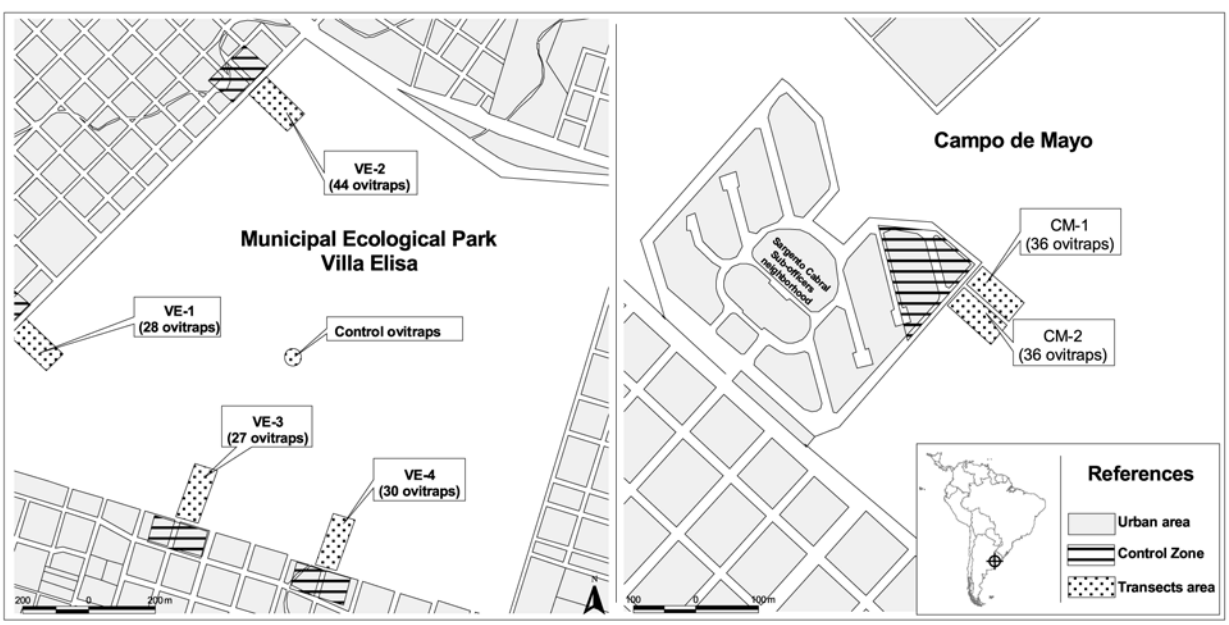

Fig. 1: Experimental zones. Representative scheme of CM and VE zones.

It is a sylvan recreational park of 200 ha of a prairie dominated by grasses, Honey Locus (*Gleditsia triacanthos*) and Ligustrum (*Ligustrum sinence*). On the border of the park and adjacent to the residential houses four areas were selected, all considered auspicious to *Ae. aegypti*, but with differences in vegetation and shade. Each of the four zones had an associated reference area in the residential zone. A total of 48 ovitraps were distributed. Two extra control ovitraps were placed at the headquarters of the park located close to the center of the park (between 600 and 1200 m from the houses). Spread across the four areas of the park 130 ovitraps were arranged in regular grids with 5 m spacing (3–4 columns, 8–12 rows), extending to a distance between 35 and 65 m of housing. Zones labeled as VE-1 and VE-2 had a street as an obstacle for dispersal (not monitored) and both were wooded. Zone VE-2 was next to the rest area following a footpath into the park. Zones VE-3 and VE-4 were crossed by a ditch (6 m wide and 2 m deep). Shadow was very scarce in zone VE-3 while VE-4 began with long grass running into a dark forest. All VE zones were separated from each other several 10 of metres.

The second location selected was Campo de Mayo (CM), a military installation of 5000 ha, at San Miguel county (34° 32' S and 58° 39' W). Campo de Mayo, being the urbanization-associated with a residential neighborhood (Barrio Sargento Cabral) for military personnel. The general location is the blend of small residential zones, military installations, wooded and crop areas, surrounded by a larger urbanization. The Barrio Sargento Cabral was considered the breeding area of the mosquito and consequently was used as reference zone. It is characterized by low houses with gardens partially wooded where grasses predominate over 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 grids. The zones were delimited by a pre-existing fence that prevents access to the people. The zones labeled as CM-1 and CM-2 present different characteristics. CM-1 is wooded and dominated by Chinaberry (*Melia azedarach*), Ligustrum (*Ligustrum sinence*), and Tala (*Celtis tala*) with sparse understory. CM-2 has a sector, close to the households, that is wooded (like zone CM-1) followed by grassland often flooded by rainwater, with scarce upland areas shaded by tall grass. In the wild environment, transects were drawn from the households, equally spaced every 10 m—four transects each in CM-1 and CM-2. In each transect nine ovitraps were placed, spaced every 5 m and running into the field 10 to 55 m off the housing (Fig. 1).

Ovitrap monitoring was performed weekly during March–April 2010 (8 wk). Oviposition was monitored using conventional black glass jar ovitraps. Each trap, with a capacity of 330 ml, contained 100 ml of clean water and a 2 × 10 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 (50 x) and *Ae. aegypti* eggs were identified and counted. The wild location was previously surveyed and the complete absence of containers that could interfere with the experience was assured.

Both the locations of study are in the same climatic region at a distance of 67 km from each other located in the metropolitan area of Buenos Aires and the arrangement of grids was conducted in wilderness areas adjacent to low density residential areas. In both the experiments, we studied the border of mosquito breeding areas. These conditions allowed us to consider both experiments as replicas.

Dispersal activity

Each ovitrap was identified uniquely by its placement and records of the number of eggs in the trap identified each week during the campaign were kept. As an intuitive indicator of dispersal distance we considered the "maximum distance", i.e. the longest distance into the wild where a positive trap was found for each grid. The landscape (plant cover and/or ditches or flooded grassland) and disturbance (as a percentage of ovitraps lost or damaged) was annotated as well.

Ovitrap positivity

Ovitrap positivity is influenced by environmental conditions such as abundance of breeding sites and weather conditions, just to mention a couple, that change with sites and time. Thus, the statistic has to be chosen to minimize these factors, a task that can only be undertaken by considering the matter within a mathematical formulation.

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_R ovitraps in the reference zone with relative weight p_R<1, and K_x ovitraps at a sampled distance x which can be located with a relative weight $\varepsilon(x)$. We will name the weight the "quality" of the ovitrap and the target of our investigation. The quality indicates the relative preference for an ovitrap at a distance x with respect to those in the reference area. Let N be the effective total number of options for egg-laying

$$N = K_{BS}+K_R\varepsilon(R)+\Sigma_x\ K_x\ \varepsilon(x)$$

Where, *K* indicates the number of effective egg-laying sites and the subscripts stand for: Breeding sites BS, reference *R*, and distance into the wild zone, *x*. Let: $p_{BS} = 1/N$; $p_R = e(R)/N$ and $p_x = (x)/N$ be the probabilities of oviposition corresponding to a breeding site, an ovitrap in the reference zone, and an ovitrap at a distance *x* respectively. Let $p_{ne}(x)$ the probability for an ovitrap located at *x* to be negative (meaning to have no eggs trapped) $p_{po}(x)$ and the probability of being positive (with at least one egg trapped), respectively. The probability $p_{ne}(x)$ after *NO* ovipositions is:

$$p_{ne}(x) = 1 - p_{po}(x) = [(1 - \varepsilon(x)/N)]^{NO}$$

Which can be approximated for large as:

$$p_{ne}(x) = \exp[-\varepsilon(x)NO/N]$$

Thus, we obtain the basic result that for fixed *N*, the quantity is In [$p_{ne}(x)$] where In is the expression for "natural logarithm" 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, it is a measure of ELMA. The regression:

$$-\text{In}\,[\hat{p}_{ne}(x)] = -\text{AIn}[\hat{p}_{ne}(R)]$$

(Where, $\hat{p}$ is a random estimate of *p*) allows to estimate the quality factor $\varepsilon(x)$ relative to the quality of the ovitraps in the reference section, using the slope of the regression. We thus obtain:

$$A = \varepsilon(x) = <\text{In}\,[\hat{p}_{ne}(x)]> / <\text{In}\,[\hat{p}_{ne}(R)]>$$

by the law of large numbers (< > indicate average values), assuming that the choice of oviposition site does not depend on the number of ovipositions, *NO* or the total number of choices, *N*.

Egg-laying mosquito activity (ELMA)

Following the mathematical analysis, the weekly activity for each area was evaluated as minus the logarithm of the fraction of negative ovitraps at different distances into the wild zone and in the reference area. We evaluate ELMA as the number of ovipositions *NO* at a given distance with the statistics:

$$NO(x)\ \alpha - \text{In}\,[1 - p(x)]$$

Where, $p(x)$ is the fraction of positive ovitraps in the region characterized by the distance *x*. The spatial variation of oviposition activity (quality) was calculated as the regression between ELMA at the location and ELMA at the corresponding reference zone as:

$$\varepsilon(x) = <\text{In}\,[\hat{p}_{ne}(x)]>/<\text{In}\,[\hat{p}_{ne}(R)]>$$

The latter expression allows us to mix data from different weeks and nearby locations.

RESULTS

Dispersal activity data

The maximum oviposition distances are shown in Table 2 for the different sets of grids in the areas without frequent human presence (VE-1, VE-3, VE-4, CM-1 and CM-2). These fluctuate between 20 and 40 m from the construction line, while in the most disturbed grid (VE-2), it was recorded at 65 m, further away from the urbanization.

In CM, neither ELMA was detected at the grassland sector nor at the tall-grass 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, up to a maximum distance of 40 m. There was no oviposition at greater distances despite maintaining the structure of vegetation.

Egg-laying activity in the reference areas

The ELMA detected at the different reference 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 (Fig. 2). In both the ovitraps placed at the center of the park (VE experiment), no ELMA was detected.

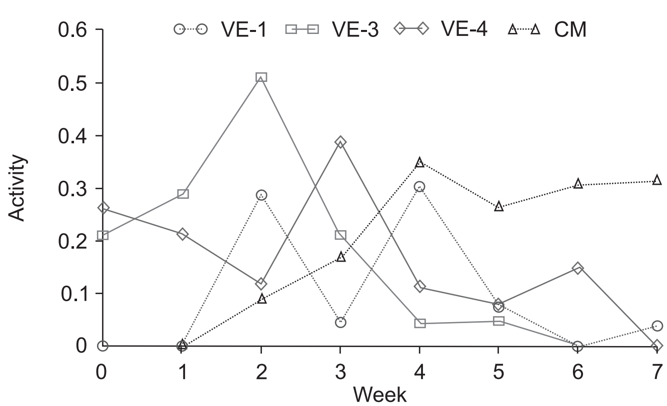

Fig. 2: Oviposition activity at the reference zones of the undisturbed grids as a function of time for the grids VE-1, VE-3, VE-4 and CM.

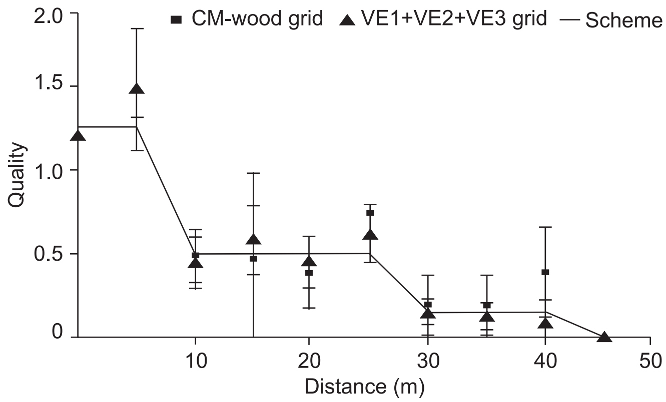

Fig. 3: Relative activity as a function of the distance to the construction line (control zone) collecting observations in undisturbed VE zones and wooded areas in CM-1 and CM-2. The quality indicates the relative preference for an ovitrap at a distance *x* with respect to those in the reference area. Error bars correspond to the standard deviation.

Egg-laying activity in the grids

We computed the quality (preference) factor as it changes with the distance to the urbanization. We found three dispersal levels: 0–10 m, 10–25 m, and 30–40 m (distances are referred to the construction line) (Fig. 3). In both the experiments, we observed that the tree cover favors the dispersal of *Ae. aegypti*. Additionally, we observed that the ditch in VE-3 and VE-4 (4 m wide, 2 m deep) is not an insurmountable obstacle.

DISCUSSION

The present results are consistent between two independent replicates performed, as well as with previous results using natural methods[10, 15]. Natural dispersal is measured with pre-existing mosquito populations, which are born and dispersed from the micro-environments of original breeding (without capturing or manipulating individuals). The only alteration produced in the environment consists in adding some egg-laying opportunities, particularly in an adjacent wild space, which eventually may induce the mosquitoes to explore the area. This is not too different from reality, because in such peri-urban environments there is often trash that can accumulate water.

Our results indicate that *Ae. aegypti* explores the area surrounding its breading sites searching for oviposition sites. The ELMA decreases with the distance to the building line. Between 5 and 10 m away ELMA drops to half of the activity in the reference urban zone. About 30 m 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 40 m. These results suggest that the dispersal distances for *Ae. aegypti* are short, in agreement with Getis *et al*[18].

Table 2. Environment and flight dispersal of *Ae. aegypti*

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 *Ae. aegypti*. VE: Villa Elisa experiment; CM: Campo de Mayo experiment; H-disturbance = Percentage of ovitraps lost; *Some Eryngium (Apiaceae) were found and explored, with negative results for *Ae. aegypti*. Indeed, leaf axils of Eryngium do not host *Ae. aegypti* but some *Culex* species[29].

The landscape has an impact in the dispersal pattern[9, 21]. We observed that a wooded plant cover appeared to facilitate dispersal and created corridors for the mosquito (Table 2). The results suggest that human activity facilitates short range dispersal as well. In contrast, the mounds shaded by tall-grass in the often flooded grassland are avoided by *Ae. aegypti*. This suggests that for control situations the degree of environmental advantage (quality) and anthropic disturbance of the target area should be considered.

The method of measurement proposed has several advantages and some obvious inconveniences. Main advantages: it does not introduce new vectors to the area, but rather eliminates a few of them in the form of eggs; the initial conditions of the experiment are not singular and, thus, do not introduce spurious 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[30]; and influence of the preparation of the mosquitoes (breeding, marking, etc). In contrast, the main difficulty encountered 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 on human movements in the dispersal of *Ae. 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, yet the proposed method presents little sensitivity to such variations.

CONCLUSION

The method gives consistent results between independent realizations of the experiment. It allows exploring questions such as the influence of breeding sites availability on dispersal. 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 reference zone and in the grids, thus allowing to cancel, with a proper choice of statistics, the influence of these factors over the relative activity.

Low repetitive 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 40 m away from the peri-domicile, its activity decreased as the distance to the urbanization decreases. A small zone, up to 5 m in the grid, presents an activity comparable to the reference area (1.25 relative activity). The activity decreased to 0.5 in the 10–25 m zone, and further decreased to 0.15 at the 30–40 m zone. No oviposition was detected beyond this distance in the grids not disturbed by human activity. When human activity was present, the maximum distance detected was 65 m, suggesting that human presence influences the dispersal. Plant cover was a determining factor for dispersal, its absence appears to deter it (grassland with scarce tall-grass) while the presence of woods makes a sort of corridor for dispersal.

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