

Modelling arthropod active dispersal using Partial differential equations: the case of the mosquito *Aedes albopictus*

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ABSTRACT

Dispersal is an important driver for animal population dynamics. Insect dispersal is conventionally assessed by Mark-Release-Recapture (MRR) experiments, whose results are usually analyzed by regression or Bayesian approaches which do not incorporate relevant parameters affecting this behavior, such as time dependence and mortality. Here we present an advanced mathematical-statistical method based on partial differential equations (PDEs) to predict dispersal based on MRR data, taking into consideration time, space, and daily mortality. As a case study, the model is applied to estimate the dispersal of the mosquito vector *Aedes albopictus* using data from three field MRR experiments. We used a two-dimensional PDE heat equation, a normal bivariate distribution, where we incorporated the survival and capture processes. We developed a stochastic model by specifying a likelihood function, with Poisson distribution, to calibrate the model free parameters, including the diffusion coefficient. We then computed quantities of interest as function of space and time, such as the area travelled in unit time. Results show that the PDE approach allowed to compute time dependent measurement of dispersal. In the case study, the model well reproduces the observed recapture process as 86%, 78% and 84% of the experimental observations lie within the 95% CI of the model predictions in the three releases, respectively. The estimated mean values diffusion coefficient are 1,800 (95% CI: 1,704–1 896), 960 (95% CI: 912- 1 128), 552 (95% CI 432–1 080) m²/day for MRR1, MRR2 and MRR3, respectively. The incorporation of time, space, and daily mortality in a single equation provides a more realistic representation of the dispersal process than conventional Bayesian methods and can be easily adapted to estimate the dispersal of insect species of public health and economic relevance. A more realistic prediction of vector species movement will improve the modelling of diseases spread and the effectiveness of control strategies against vectors and pests.

1. Introduction

Animal dispersal refers to movements away from the place of birth towards another location for reproduction. The main drivers of dispersal are related to the avoidance of kin competition and inbreeding and escaping deteriorating environmental conditions (Bowler and Benton, 2005). In the case of insects, assessing the active dispersal range might be of crucial importance particularly in the case of species which damage agricultural productions, unsettle ecosystems, and threat human health. Among more than 6 million species of insects known, only less

than 100 are either important pests for major crops or relevant vectors of human and/or animal diseases. The deep knowledge of these species dispersal is instrumental to develop proper integrated pest management plans which maximize cost-effectiveness of interventions and protect the environment in a sustainable way.

Although many theoretical models are available, empirical studies are generally lacking due to the difficulties of linking observations to the quantification of dispersion (Tesson and Edelaar, 2013). Advanced satellite radio telemetry and acoustic are giving new opportunities to study dispersion of big size animals such as large mammals or sharks

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(Cagnacci et al., 2010; Spaet et al., 2020), but are less useful to quantify the dispersal of small animals. In the case of insects, Mark-release-recapture (MRR) is the most widely used technique for quantifying dispersal: specimens are first collected/reared and marked, then released from a single site and subsequently recaptured through traps placed at different distances in a given study area (Pollock et al., 1990).

The most common statistical approaches used to estimate dispersal from MRR data are regression techniques which aim to estimate the mean distance travelled (MDT) and the flight range (FR_x) of a specified fraction \underline{x} of the population, rather than the diffusion process of individual marked specimens. Other methods to estimate insect dispersal follow a Bayesian framework which explicitly models the diffusion process (Villela et al., 2015). For instance, the hierarchical Bayesian model proposed by Villela et al. (2015) for the mosquito *Aedes aegypti* takes advantage from the flexibility of the Bayesian approach and expands the frequentist approach by including three components: two probabilistic models, describing the spatial distribution of specimens and the daily survival of marked and native individuals, and an observation model describing the sampling process.

Partial Differential Equations (PDEs) represent a standard mathematical method to model diffusion processes, such as the gas dynamics and heat distribution (Borthwick et al., 2016). In ecology, PDEs have been applied to study spatial-temporal dispersal of animal populations in a continuous domain (Bassett et al., 2017; Kareiva et al., 1990), such as the home-range dynamics of meerkats (*Suricata suricatta*) (Bateman et al., 2015) and the dispersal of butterflies (Ovaskainen, 2004).

The aim of this work is to provide a PDE-based analytical method to estimate insect dispersion based on MRR field data. This method, compared to previously quoted ones, allows to estimate the dispersion taking into account the daily mortality of marked release insects and the days after release (time) in a single mathematical equation. In particular, we applied the proposed modeling framework to estimate the dispersal of blood-fed females of the tiger mosquito, *Aedes albopictus*, during the egg laying phase. This species represents a significant public health burden due to its capacity to transmit exotic arboviruses, such as dengue (DENV) and chikungunya (CHIKV), capable of induce serious diseases in humans (Zeller et al., 2016). The species was the primary responsible of the thousands of DENV cases recorded in the southwest of the Indian Ocean in 2015–2018 (Vincent et al., 2019) and of the first autochthonous cases of both viruses in Europe (Marrama Rakotoarivony and Schaffner, 2012), where it caused two large CHIKV outbreaks with hundreds of human cases (Italy 2007 and 2017; Caputo et al., 2020).

We expect that the proposed approach can be applied to quantify dispersal, and hence improve control of diseases transmitted by *Ae. albopictus* and by other mosquito species of global relevance (such as the major arbovirus vector, *Ae. aegypti*, and malaria vector species), as well as of agricultural pest species.

2. Materials and methods

2.1. Modelling

Our model expands the one proposed in (Lutambi et al., 2013). Precisely, we included in the main equation the mortality and capture processes of the species of interest. Thus, the equation assumes the following form:

$$\frac{\partial M}{\partial t} = D \left(\frac{\partial^2 M}{\partial x^2} + \frac{\partial^2 M}{\partial y^2} \right) - M(\mu + \beta) \quad (1)$$

Where μ is the mortality rate, β is capture rate, (x, y) represent location coordinates as distance (in meters) along the x and y spatial axis from a given origin (x_0, y_0) respectively, t is the time (i.e., days or hours), $M(x, y, t)$ is the density of the population of interest (individuals/m²) at location (x, y) at time t . In the equation [1] we assume that the initial number of

individuals are $M(x, y, 0) = M_0 \delta(x, y)$ where $\delta(x, y)$ is the Dirac delta function in two dimensions so $\delta(x, y) = 0$ for $x^2 + y^2 \neq 0$ and $\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \delta(x, y) dx dy = 1$ and therefore, $\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} M(x, y, 0) dx dy = M_0$. The number of specimens in a general rectangular $S = [0, a] \times [0, b]$, is given by $\int_S M(x, y, t) ds$.

The term $\left(\frac{\partial^2 M}{\partial x^2} + \frac{\partial^2 M}{\partial y^2} \right)$ indicates the diffusion in space and D is the diffusion coefficient that measures dispersal rate (distance²/time). In addition, we assumed Neumann boundary conditions i.e., $\frac{\partial M}{\partial x}(0, y) = \frac{\partial M}{\partial x}(L, y) = 0$ and $\frac{\partial M}{\partial x}(x, 0) = \frac{\partial M}{\partial x}(x, L) = 0$. This implies that we assumed neither immigration (which is reasonable considering that we are modelling only the dispersal of released mosquitoes) nor emigration of mosquitoes from the study area (such assumption should be accounted for in the study design when selecting the sampling area). The analytical solution of [1], as shown in (Lutambi et al., 2013), is:

$$M(x, y, t) \sim Norm((R_x; R_y), \Sigma) * M_0 e^{-(\mu + \beta)t} \quad (2)$$

Where *Norm* is bivariate normal distribution, $(R_x; R_y)$ is the distance on the x and y axis from the initial point (x_0, y_0) , and Σ is the following 2×2 covariance matrix:

$$\Sigma = \begin{pmatrix} \sigma_{xx}^2 & \sigma_{xy}^2 \\ \sigma_{yx}^2 & \sigma_{yy}^2 \end{pmatrix} \quad (3)$$

Here, we suppose that x and y are independent, meaning that the diffusion process is equal with respect to x and y , thus: $\sigma_{xy}^2 = \sigma_{yx}^2 = 0$; $\sigma_{xx}^2 = \sigma_{yy}^2 = 2Dt$. In other words, we assume that the movement of the species of interest follows a Brownian motion (Lutambi et al., 2013), meaning the diffusion coefficient D is equal for both x and y directions. In our case, the bivariate normal distribution models the probability of finding specimens of the species of interest in a point (x, y) at time t .

While our model was developed to estimate the diffusion coefficient of a selected species, it could also have other unknown parameters such as the mortality or the capture rate. We denote the set of free parameters with θ . Different techniques can be used to estimate θ , for instance, Markov chain Monte Carlo (MCMC), maximum likelihood, and particle filtering (Gelman et al., 2013).

2.2. Case study

We apply the proposed model to estimate the dispersal of blood-fed *Ae. albopictus* females using MRR field data. The entomological data were collected through three MRR experiments carried out on August 3rd (MRR1, N released females = 1049), August 24th (MRR2; N = 1600) and September 9th (MRR3; N = 1200) 2009 in the municipality of Piove di Sacco (Padua province, Veneto, northeastern Italy) (see Marini et al., 2019), for a detailed description of the experiments). In brief, blood-fed females were released from a single site and recaptures were carried out by 96 sticky-traps (STs, Facchinelli et al., 2007) distributed within 10 concentric 50m-radius annuli around the release site (see Table S1 in the Appendix). Data used in the model refer to daily recaptures of marked mosquitoes carried out in the first five consecutive days after release, i. e., 76 during MMR1, 183 during MMR2 and 29 during MMR3 (see Table S2 in the Appendix).

Mosquito mortality value used in the model is based on results of an assessment carried out on marked mosquitoes under semi-field conditions in parallel with the MRR experiments (see Table S3 in the Appendix). Empirical data were fitted with several functions: (i) $M_0 e^{-\sigma t}$ exponential, (ii) $e^{-\frac{A}{B}(1 - e^{-Bt})}$ Gompertz, (iii) $e^{-\frac{c}{d}t^d}$ Weibull, (iv) $\frac{e^{a+bt}}{1 + e^{a+bt}}$ GLM; where t is day of experiment and M_0, σ, A, B, c, d are free-parameters estimated through the nlsLM (Non-Linear Square Levenberg-Marquardt) method (see Table S4 in the Appendix) and a (Intercept), b estimated through the Generalized Mixed Model using Binomial distribution (see Table S5 in the Appendix). We computed the likelihood of

daily mosquito mortality, which is assumed to follow a binomial distribution, for each tested function. In addition, we evaluated the Root Mean Square Error (RMSE) for each function to quantify differences between predicted and observed values. Finally, we selected the best function for mortality considering both measures. So, in this case study we remark that the mortality rate μ is a function of time t .

The capture rate β is defined as $\beta = \alpha * \frac{N \bullet A}{A_s} * \zeta$, where α is the average daily capture rate of a single sticky-trap. Here, α (estimated value = $1.24 \cdot 10^{-4}$) has been computed using field data from three different MRR experiments carried out in Rome (Italy) in 2009, in which the same sticky-traps were used to recapture *Ae. albopictus* females (Marini et al., 2010). The parameter α is defined as the number of recaptured marked mosquitoes divided by the product between the total number of mosquitoes released, the total number of sticky-traps deployed and the total number of days of MRR experiment. Such rate (α) was rescaled by the factor $N \bullet A / A_s$ to take into account the different density of active traps within each annulus, where N is the number of operational traps, A is the area of the inner (and smallest) annulus where a single trap was present, and A_s is the area of the annulus s . Finally, we multiplied the rescaled rate for a correction factor ζ , to be will estimated (so it is a free parameter belonging to set θ).

Thus, in our study case, the set of free parameters is $\theta = \{D_i, \zeta\}$ and their posterior distribution was estimated following a MCMC approach. We initially explored the parameter space by sampling 1000 values of each free parameter from a uniform distribution (range: 0–2). The set of parameters that best fitted the data was then used as a starting point for the MCMC algorithm.

We simulated mosquito dispersal sampling and the mosquito location at each time step (12h) from equation [2]. We assumed mosquito survival to follow a binomial process of parameters $1-\mu(t)$ and $M(t)$ where $\mu(t)$ is the computed mortality at each time step t , and $M(t)$ are the surviving mosquitoes define as $\int_S M(x, y, t) ds$ from time step t . Thus, we verify if every mosquito is alive with a binomial extraction with probability $1-\mu(t)$ given by the selected mortality function. We assumed that the number of captured adult female mosquitoes at given day t and annuli s follows a Poisson distribution with mean $\lambda_{\{t,s\}}$; therefore, the likelihood of the observed data given a parameter set θ was:

$$L \prod_{i=1}^{\varphi} \prod_{t=1}^{\Psi} \prod_{s=1}^{\Delta} \frac{e^{-\lambda_{\{t,s\}}(\theta_i)} \lambda_{\{t,s\}}(\theta_i)^{n_{\{i,t,s\}}}}{n_{\{i,t,s\}}!} \quad (4)$$

where $i \in \varphi$ are the number of replicas of the mark release experiments, $t \in \Psi$ are the consecutive days after release of MRR, $s \in \Delta$ are the number of annuli, $\lambda_{\{t,s\}}(\theta_i)$ is the expected number of captures at day t and annuli s defined as $\lambda_{\{t,s\}}(\theta_i) = \beta_i \int_S M(x, y, t) ds$ simulated by the model

with parameter set $\theta_i = (\mu_i, \beta_i, D_i, \zeta)$. Finally, $n_{\{i,t,s\}}$ is the observed number of trapped marked mosquitoes at day t ($t = 1, \dots, \Psi$) and annulus s ($s = 1, \dots, \Delta$) during experiment i ($i = 1, \dots, \Phi$).

Here we used aggregated captures from each annuli s and day t and applied a sensitivity analysis study to assess the robustness of our stochastic model. Afterwards, we considered two additional scenarios for the parameter set θ : $\theta_i = (\mu_i, D_i, \zeta)$ and $\theta_i = (\mu_i, D_i)$ that were compared using the Akaike Information Criterion (AIC) (see Table S7, Figs. S3 and S4 in the Appendix). In addition, we assumed a different likelihood function under the hypothesis that the capture process followed a Negative Binomial distribution rather than a Poisson distribution (see Eq. (1) in Additional results section in the Appendix).

A total of 15,000 MCMC iterations with a burn-in of 5000 were performed and the convergence was checked by visual inspection on the trace plots of chains. Finally, we simulated 1000 releases, using the estimated parameters (D, ζ) discarding the first 5000 MCMC iterations, to compare our model predictions with the observed data. All statistical analysis and model simulations were performed using the statistical software R version 3.6.1 (R Foundation for Statistical Computing., 2018) and packages tidyverse (Wickham, 2017), mvtnorm (Ekström, 2010).

The R code and the data are available at <https://github.com/Chia1992/Partial-Differential-Equation>.

As mentioned in the introduction, a standard method to quantify the dispersal is measuring the flight range (FR). The FR measures the area travelled/covered by marked mosquitoes in a unit of time. Classical methods, such as the regression model, estimate the FR with the cumulative number of expected recaptures at the end of the MRR experiment (Lillie et al., 1985; Morris et al., 1991; White and Morris, 1985), while the PDE method used the daily recapture. We used the parameters obtained by MCMC approach and the equation [2] to calculate the FR, thus the equation is:

$$FR = Norm\left((R_x; R_y), \sqrt{2Dt}\right) M_0 e^{-\mu} \quad (5)$$

FR₅₀ (area travelled by 50% of marked mosquitoes) and FR₉₅ (area travelled by 95% of marked mosquitoes), were calculate from the equation [5] considering 50% and 95% of marked mosquitoes that are found each day t in the annulus s .

3. Results

In this section we present: (i) the estimated values for the diffusion coefficients (D_1, D_2, D_3 for MRR1, MRR2 and MRR3 respectively), the correction factor (ζ) and the daily mortality rate (μ_1, μ_2, μ_3 for the first, second and third semi-field experiments); (ii) the simulation of the dispersal process of the marked mosquitoes during five consecutive days after release; (iii) a validation of the mathematical-statistical model proposed here using the analytical solution of equation [2].

3.1. Diffusion coefficients and correction factor (D, ζ)

The diffusion coefficients estimated by the stochastic model vary among the three MRR experiments. The mean values are 1800 (95% CI: 1716–1907), 983 (95% CI: 912–1143), 564 (95% CI 442–1103) m^2/day for the MRR1, MRR2 and MRR3 experiment respectively (see Table S6 and Fig.S1 in the Appendix), which can be interpreted as the area covered in a day by the dispersion process of the mosquitoes, i.e., the area travelled by the mosquitoes. The mean value of the correction factor (ζ) for the capture rate of sticky-traps is 81.35 (95% CI: 72.47–88.44) (see Table S6 and Fig.S1 in the Appendix Our model well reproduces the marked mosquito recapture observed dynamics, with 86%, 78%, 84% of the experimental observations lying within 95% of the model predictions in the first, second and third releases, respectively (Fig. 1).

The estimated mean diffusion coefficient allows to evaluate the flight ranges over time. In MRR1, the predicted FR₉₅ is on average 163 m (95% CI: 155–171 m) at day 1 and increases up to 361 m (95% CI: 342–382 m) at day 5 after release, whereas in MRR2 and MRR3 the FR₉₅ start from 119 m (95% CI: 115–124 m) and 91 m (95% CI: 87–96 m) and increase up to 267 m (95% CI: 256–280 m) and 204 m (95% CI: 194–213 m) in the first and fifth day after release, respectively (Fig. 2).

To validate the stochastic model, we compared the predicted density of marked *Ae. albopictus* females with the analytical solution of the PDE (equation [2]). As shown in Fig. 3, there is a very good agreement between the analytical solution and model simulations: 68%, 86%, 100% of the analytical results are within 95% of the simulated model data in MRR1, MRR2 and MRR3, respectively.

3.2. Mortality rate estimate

The comparison of the considered mortality functions shows that the exponential and the Weibull functions provide the best fit (higher likelihood) of the mortality data of marked mosquito in the semi-field experiment (see Table 1 and Fig.S2 in the Appendix).

The functions with the highest values of likelihood (Exponential and Weibull) were compared by means of a likelihood ratio test. Since no

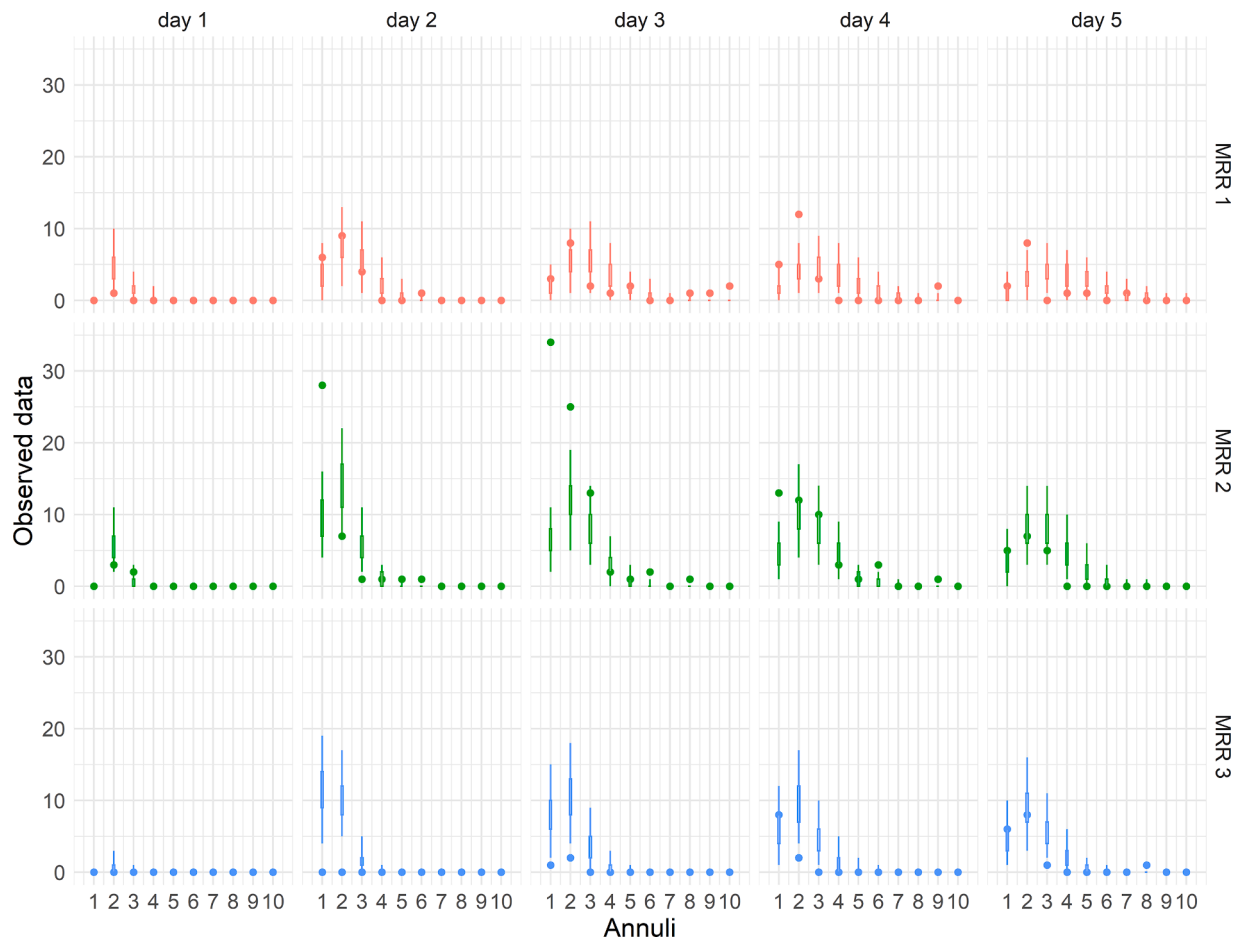


Fig. 1. Model fit. Boxplot (2.5%, 25%, 75% and 97.5% quantiles) of the number of recaptured marked mosquitoes predicted per annulus (each annulus 50 mt) by the model (boxplots representing the 2.5%, 25%, 75% and 97.5% quantiles) for each MRR experiments (rows: MRR1 red, MRR2 green, MRR3 blue) in the first five days after release (columns). Dots represent the number of marked mosquitoes recaptured during the MRR experiments.

statistical differences were observed between Exponential and Weibull likelihood value (p -value = 0.21, $df = 1$), the exponential function was chosen, given its simpler formulation compared to Weibull. The estimated daily mortality rates using the exponential function were 2.1%, 1.8%, 1.3% in MRR1, MRR2 and MRR3, respectively.

4. Discussion

Here we presented a PDE-based stochastic framework to estimate insect dispersal based on MRR data. We tested it in a specific case-study to overcome the limitations of the commonly used analytical approaches, i.e. regression analysis (Marini et al., 2019) and hierarchical Bayesian models (Vilella et al., 2015). Indeed, the big advantage in the use of PDEs is the possibility of including time, space, and daily mortality in only one mathematical equation, thus providing a more realistic representation of the dispersal process, which could improve the planning of control activities of human vectors and agricultural pests, as well as the study of their collective behavior.

We applied the PDE method to study the dispersal of *Ae. albopictus*, which represents a major source of nuisance and a public health threat also in temperate regions, in order to highlight the potential of PDE approach in studies aimed at predicting the transmission dynamics of vector-borne pathogens and at planning vector control interventions. We exploited data from three MRR experiments, during which daily mortality rates of marked mosquitoes were experimentally estimated under semi-filled conditions. A good agreement between the stochastic model and observed data was observed. Moreover, given the analytical solution, the calculation of quantities of interest such as FR is

straightforward. It is important to stress the implication that such result may have on control strategies, as it may allow to tailor the spatial radius deemed necessary to target the population of interest (Marini et al., 2019; Yamashita et al., 2018).

In the case study, the FR_{95} resulting from the PDE approach is significantly higher than the one estimated using regression analysis (Marini et al., 2019), i.e. 361 m, (95% CI: 342–382 m) vs 250 m in MRR1, 267 m (95% CI: 256–280 m) vs 209 m in MRR2, and 204 m (95% CI: 194–213 m) vs 177 m in MRR3. This is due to the inclusion in the analysis of daily mortality and time (day after release) and is thus expected to be more realistic. The spatio-temporal patterns of *Ae. albopictus* blood-fed females modelled through the PDE approach suggest that the dispersal increases over time, a conclusion which could not be reached using a conventional regression approach (Marini et al., 2019).

The latter result suggests that in case of arbovirus transmission, the size of the area covered by vector control interventions should change over time to target the same fraction of the mosquito population potentially involved in the transmission event. For instance, in Italy, it is recommended that in case of autochthonous arbovirus transmission, vector control intervention (i.e. insecticide sprayings, larvicide application, door-to-door activity) are carried out in a 100 m buffer around the residence of a suspected or confirmed case (Ministero della Salute et al., 2019). Our model estimates that the probability of a mosquito being within this buffer is equal to 0.88 and 0.5 after 24 h and 3 days from the potentially infectious blood meal, respectively.

Indeed, the flight range estimated for all MRR experiments suggested a very rapid dispersal, as in the case of MRR1 when 95% of mosquitoes travelled beyond 163 m (95% CI: 155–171 m) 1 day after release and

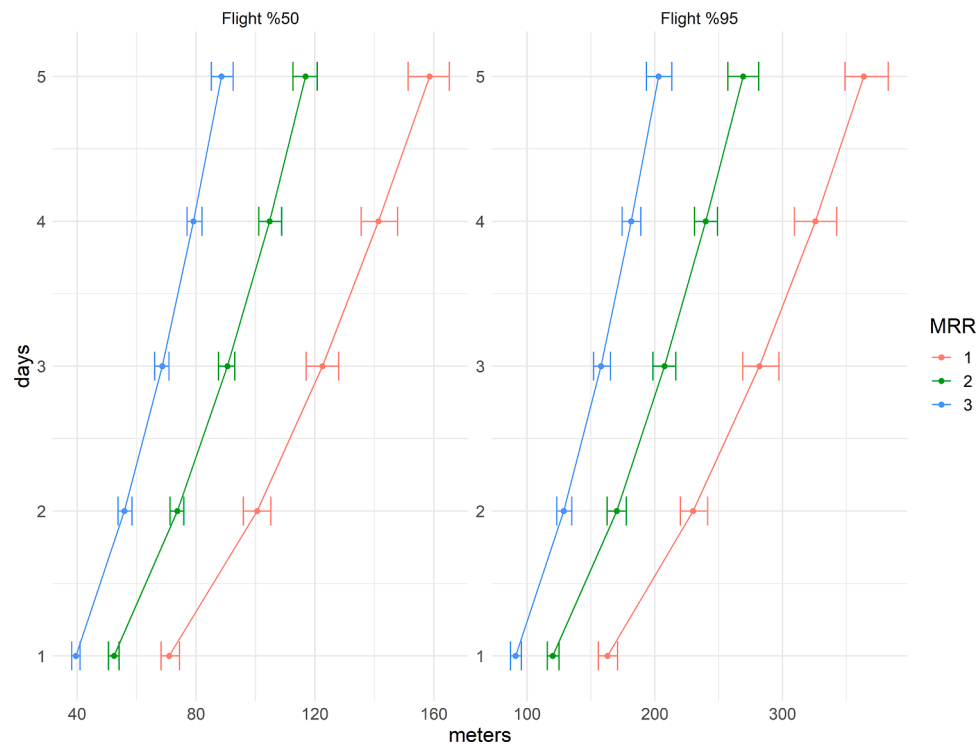


Fig. 2. Flight range of marked blood-fed females of *Aedes albopictus* estimated by the model (meters/day traveled by 50% and 95% of mosquitoes). Dots represent the average predicted distance (in meters) from the release point covered by 50% (left panel, i.e., FR50) and 95% (right panel, i.e., FR95) of marked mosquitoes for MRR1 (red), MRR2 (green), and MRR3 (blue). The segments represent the 2.5–97.5% quantiles. x-axis: Meters, y-axis: days after release.

over 361 m (95% CI: 342–382 m) 5 days after release.

Standard regression approaches for the computation of the flight range do not take into account time dependency but model cumulative captures, over the entire study period, as a function only of the distance. It should be noted that, given the short time span of the recapture data in our MRR dataset (5 days) and the low observed mortality, we did not need to make any assumption on the spatio-temporal variation of diffusion coefficient. However, in the PDE we assumed that mosquito dispersal is homogeneous in space (with respect to x and y coordinates) and temporally constant. It would be interesting in the future to address the spatio-temporal dependency of the diffusion parameter D (i.e., individuals of the species will not disperse indefinitely, nor randomly). In addition, we included in the model estimates of capture and daily mortality rates, which may be difficult to be estimated under different experimental conditions. In our study we calibrated the capture rate, evaluated by [Marini et al., \(2019\)](#), to our data by estimating the correction factor (ζ). It is important to remark that if the mortality and capture rate are not available, they can be considered as free parameters and thus can be estimated by the stochastic model. Adding these free parameters into the model would increase the complexity of the model.

Finally, our proposed framework could be improved by including other parameters affecting insect dispersal, such as wind ([Bowen et al., 1991](#); [Cummins et al., 2012](#); [Knols and Meijerink, 1997](#); [Raffy and Tran, 2005](#); [Smallegange et al., 2005](#)), provided that they are appropriately estimated during the MRR experiments. Indeed, differences either in wind direction and force, or in other meteorological features, might account, at least partially, for the different estimates in the diffusion coefficients between the three MRR experiments, as hypothesized in [Marini et al., \(2019\)](#).

It is critical to highlight that estimate obtained from our analytical approach are unavoidably affected by the experimental design (e.g., the physiological stage of marked insect, the ecology of the site of release and recapture, the size of study areas, the recapture methods). FR_{90} estimates for *Ae. albopictus* are higher in a study conducted in Switzerland ([Vavassori et al., 2019](#)) compared to ([Marini et al., 2019](#)).

However, the experimental design of the two studies largely differ: i) freshly emerged adults instead of blood-fed females were released in Switzerland; ii) BG-Sentinel trap instead of blood-fed ones were released in Switzerland to focus on dispersal triggered by host-seeking, rather than by egg-laying; iii) the study area was larger in Switzerland (1 km radius instead of 500 m). Application of PDE method to this dataset could allow a more realistic comparison of the two datasets.

Epidemiological models are used to evaluate the risk of outbreaks occurrence and, more generally, to study the circulation, possibly spatial and temporal, of a given mosquito-borne pathogen ([Li et al., 2021](#)). Most of these models include into the equations various parameters that can influence the transmission of pathogens such as the vector mortality and oviposition rates and the length of gonotrophic cycle (e.g. [Poletti et al., 2011](#); [Otero et al., 2006](#); [G. Marini et al., 2019](#)). The dispersal of mosquitoes can be incorporated into these models by introducing either the dispersion term or the value of the diffusion coefficient (D) estimated in this work. In fact, during an outbreak, mosquito dispersion might be an important factor. Seventy percent of focal infections during a large chikungunya outbreak mediated by *Ae. albopictus* in the Lazio region (Italy) in 2017 were transmitted within a distance of 200 m, demonstrating the key importance of the dispersal of infected mosquitoes in the spatial spread of mosquito borne diseases ([Guzzetta et al., 2020](#)). Finally, our results on the dispersion of mosquitoes could be useful both for models aimed at predicting mosquito abundance ([Zheng et al., 2018](#)) and for models carried out to evaluate demographic effects of SIT techniques ([Haramboure et al., 2020](#)).

5. Conclusions

The results here obtained are useful for the definition of the optimal buffer on which to focus emergency mosquito-borne virus control interventions (i.e. deployment of adulticides insecticides aimed at eliminating potentially infected mosquitoes in the area surrounding the residence of an arbovirus infected person). This information is crucial for public authorities, as it has already been shown that enlarging the

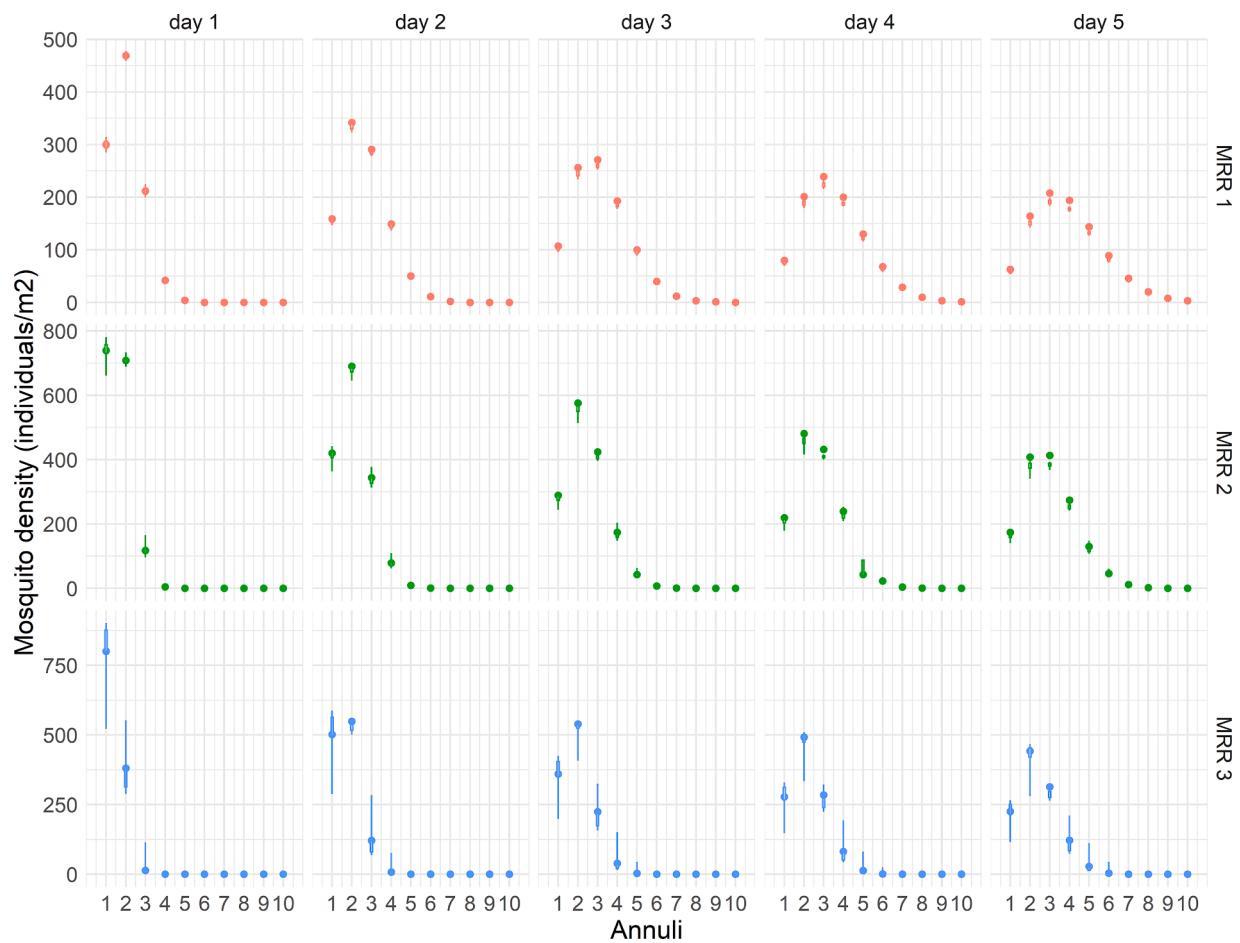


Fig. 3. Comparison between mosquito density (mosquitoes/m²) predicted by the analytical solution and the model. Number of mosquitoes predicted per annulus by the analytical solution (dots) and by the stochastic model (boxplots representing the 2.5%, 25%, 75% and 97.5% quantiles) for each day (in columns) and MRR experiment (in rows, MMR1: red, MRR2: green, MRR3: blue).

Table 1

Summary of RMSE and likelihood for the four mortality functions of marked mosquitoes in semi-field condition. The values represent the sum of three MRR experiments (RMSE = Root Mean Square Error).

| | Exponential | Gompertz | Weibull | GLM |
|------------|-------------|----------|---------|-------|
| RMSE | 0.062 | 0.057 | 0.053 | 2.58 |
| Likelihood | -65.69 | -67.79 | -64.93 | -72.2 |

size of the area to be treated and reducing the time interval between infective case identification and the control implementation might substantially increase the effectiveness of the intervention during an arbovirus outbreak (G. Marini et al., 2019).

The mathematical/statistical framework developed here can be easily adapted to estimate the dispersal of other insect species of public health and economic relevance. Indeed, MRR data are available for major arbovirus (i.e., *Ae. aegypti*, (e.g. Villela et al., 2015)) and Afro-tropical malaria vectors (e.g. Epopa et al., 2017), as well as for agricultural pest species, such as *Drosophila suzukii* which damages the fruit during the ripening stage (Asplen et al., 2015), or the beetle *Platypus koryoensis*, vector of the fungus *Raffaelea quercus-mongolicae*, which is fatal for oaks (Lee et al., 2019).

6. Data availability statement

The R code and the data are available at <https://github.com/Chi1992/Partial-Differential-Equation>

CRediT Author Statement

Chiara Virgillito: Methodology, Data curation, Writing. **Mattia Manica:** Methodology, Data curation, Writing. **Giovanni Marini:** Methodology, Data curation, Writing. **Beniamino Caputo:** Collecting data, Writing. **Alessandra della Torre:** Collecting data, Writing-Reviewing. **Roberto Rosà:** Methodology, Data curation, Writing-Reviewing.

Declaration of Competing Interest

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

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2021.109658](https://doi.org/10.1016/j.ecolmodel.2021.109658).

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