Sensitivity analysis of factors influencing the ecology of mosquitoes involved in the transmission of Rift Valley fever virus

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Abstract

Vector-borne diseases are a major global health concern, with Rift Valley fever (RVF) serving as a key example due to its impact on both human and animal health. Effective control and prediction of such diseases require an understanding of how environmental factors influence mosquito ecology. As mosquito abundance, distribution, and behavior are shaped by ecological conditions, identifying these drivers is essential for anticipating transmission risk and informing public health interventions. This study aims to assess the sensitivity of key factors governing the ecology of mosquitoes, using a deterministic, compartmental model developed for the transmission of RVFV in Kenya. Specifically, we investigate the influence of four model parameters on mosquito abundance, focusing on the proportion of water body area utilized for oviposition. A literature review was conducted to establish parameter ranges and distributions. The Sobol method of global sensitivity analysis was then applied to a simplified model environment, firstly with constant temperature and water body area and secondly with periodic temperature and water body area. The indices calculated were used to rank the parameters based on their influence on mosquito abundance. The analysis showed that there is a need to reduce uncertainty in the area scanned by *Culex* and identified the proportion of water body area used for oviposition as a highly influential parameter. This finding underscores the need for further research into spatial oviposition trends across different water bodies, as current literature lacks sufficient data to inform realistic parameter estimates.

Author summary

Rift Valley fever (RVF) is a disease spread by mosquitoes that affects both people and animals. Understanding what drives mosquito populations can help us predict and control the spread of RVF. In this study, we used a mathematical model to explore how different environmental factors, such as temperature and the role of water bodies, affect mosquito numbers. We focused on four key factors, where the analysis emphasizes the

role of water bodies used by mosquitoes to lay their eggs. We found that this factor plays a major role in how many mosquitoes are present. However, there is still a lot we don't know about exactly where mosquitoes choose to lay their eggs. More research in this area could improve how we predict and manage RVF outbreaks. Our findings highlight which environmental details matter most, and they can help guide better strategies for mosquito control and disease prevention.

Introduction

Rift Valley fever (RVF) is a mosquito-borne viral disease caused by the Rift Valley fever virus (RVFV), which is currently considered a priority for research and development in emergency contexts by the World Health Organization [1]. First identified in Kenya's Rift Valley in 1931 [2, 3], RVFV has since spread across Africa, with outbreaks in Saudi Arabia and Yemen in 2000 raising concerns about its geographic expansion [4]. Transmission is strongly seasonal, driven by environmental conditions that affect mosquito populations, making prediction both possible and essential. However, existing models struggle to determine which parameters most influence vector dynamics.

Kenya has experienced significant RVF activity, including a severe 2007 outbreak that devastated pastoral communities in the northeast. In Garissa alone, an estimated 300,000 animals died, triggering economic hardship across the livestock sector [5]. While RVFV primarily affects domestic ruminants, causing abortions and high mortality in young animals, it also infects humans, occasionally leading to serious complications such as ocular damage, renal failure, or hemorrhagic fever [6–8]. These impacts highlight the urgent need for effective predictive models to support RVF control.

Given the impact of RVFV on both humans and livestock, understanding its mosquito vectors is crucial for disease modelling and control efforts. Pepin et al. (2010) [9] coined terms describing the two distinct groups of RVFV vectors: 'reservoir/maintenance vectors' (i.e. primary vectors) and 'epidemic/amplifying vectors' (i.e. secondary vectors). The former group is thought to primarily consist of *Aedes* species mosquitoes, while the latter group is believed to comprise mainly *Culex* species mosquitoes, though *Mansonia* and *Anopheles* are often involved as well [10].

One key factor influencing RVFV transmission is the breeding behavior of its primary mosquito vectors. In some regions of Kenya, floodwater *Aedes* mosquitoes typically lay their eggs in dambos: grass-covered, shallow depressions which become waterlogged after rainfall [11]. Crucially, *Aedes* eggs must be submerged in water to hatch. During periods of particularly low rainfall in these areas, *Aedes* eggs will build up along the perimeter of the dambos, where they can survive desiccation for many months in a state called diapause [12]. Numbers of adult *Aedes* mosquitoes may diminish as the eggs lie dormant. When rain does eventually occur, considerable quantities of adult mosquitoes can emerge in one go as many submerged eggs are allowed to develop simultaneously. A proportion of these may be infected with RVFV, due to the ability of *Aedes* mosquitoes to vertically transmit the virus to their eggs [13]. Thus, this mass emergence of adults sets up a scenario where RVFV outbreaks are particularly likely [14].

A deterministic, compartmental ecoepidemiological model of RVFV transmission [15] captures key disease-environment interactions, but lacks clarity on the relative influence of specific ecological parameters, prompting this study's focus on sensitivity analysis to better understand the drivers of mosquito abundance. Our analysis is conducted in a simplified setting, focusing on vector ecology and initially excluding fluctuations in temperature and water body area. We focus on four key parameters with uncertain values in the literature, aiming to determine which have the greatest influence on model outcomes. Identifying these influential parameters will help prioritize research efforts and allocate resources more effectively.

Our findings highlight a significant knowledge gap surrounding spatial patterns of mosquito oviposition across larger bodies of water. If more accurate estimates of these parameters were available, this could improve both the accuracy and usefulness of mathematical models of mosquito-borne disease such as ours.

Materials and methods

Literature review search methodology

A scoping review was carried out to obtain (for each of the four parameters of interest) a range of potential values and a distribution within that range. A literature search was conducted on PubMed to identify studies related to the reproductive behavior and ecology of key RVFV vector mosquitoes in Kenya. The search terms included keywords related to oviposition and fecundity, combined with specific *Aedes* (*circumluteolus, mcintoshi, ochraceus, pembaensis, sudanensis, dentatus*) and *Culex* (*poicilipes, quinquefasciatus, univittatus, zombaensis, bitaeniorhynchus, pipiens*) species, as well as behavioral and ecological aspects of these vectors [16]. We searched the literature from 1966 to 2024 and considered only articles written in English.

The initial search yielded 169 results. Screening of titles reduced this number to 68, and further examination of abstracts narrowed the selection to 48 relevant studies. After a detailed review of the full texts, eleven papers were ultimately included in the analysis. These studies provided critical insights into the reproductive and ecological traits of RVFV vector species, aiding in a more profound understanding of their role in disease transmission dynamics. Eight more publications were included from citation searches. The results of this review have been used to carry out a sensitivity analysis using Sobol's method of sensitivity indices [17]. We then further investigate the mechanisms behind these indices (see below).

Model assumptions

The model assumes that mosquito development and mortality are both dependent on the life stage of the mosquito and the temperature [18,19]. A detailed description of the model and its functions can be found from the supplementary material in Lo Iacono et al. (2018) [15]. The enhanced code used within this analysis is available via GitHub [20].

Parameter quantification

This model is set up to receive daily empirical data for air temperature, water body area, and livestock numbers. Firstly, to allow for more transparent analysis, we removed some layers of complexity, imposing a constant temperature, constant water body area and constant livestock number. Nevertheless, we set up three levels of temperature and water body area in case this had an impact on the results. A further parameter representing the probability of mosquitoes to find and feed on the particular host species of interest (i.e. detection probability, denoted as p_f in [15] and *prop_find* in the code) was also assigned multiple levels. For each of these three additional parameters, 'low', 'medium' and 'high' values were selected, with the temperature and water body values based on empirical datasets previously used for Kenya (see Supplementary Material [15], Figs S2-S5). The values for the parameter p_f were arbitrarily selected. These values are detailed in Table 1.

Secondly, since the oviposition rate of *Aedes* mosquitoes also relies on the fluctuations of the water body areas, i.e. the eggs are laid on soil and the flooding allows them to hatch, then the analysis was completed using periodic functions to

Table 1. Choice of constant low, medium and high parameter values for sensitivity analysis.

Parameter	low	medium	high
Temperature ($^{\circ}C$)	21	25	29
Water Body Area (m^2)	10 000	17 500	25 000
Detection Probability, p_f	0.01	0.1	0.5

denote the temperature and water bodies. These are approximated, based on empirical data, respectively, in [15] as

$$T(t) = T_m + T_A \cos(\omega_T t + \phi_T), \tag{1}$$

$$S^P(t) = S^P_m + S^P_A \cos(\omega_s t + \phi_S), \tag{2}$$

where ω_T and ω_S are the frequencies of oscillations in temperature and surface areas of water bodies; the terms T_m and S^P_m represent the mean temperature and mean surface area of water bodies during periods $2\pi/\omega_T$ and $2\pi/\omega_S$, respectively; T_A and S^P_A are the maximum amplitudes in the oscillations; and ϕ_T and ϕ_S are the respective phases.

In the sensitivity analysis, the following parameters were reviewed: i) the typical area scanned by mosquitoes looking for oviposition sites ($\mathcal{A}_C$ and $\mathcal{A}_A$ for *Culex* and *Aedes* mosquitoes, respectively); ii) the proportion of the water body area that adult female *Culex* mosquitoes lay eggs on (κ^{Culex}) and the proportion of soil that adult female *Aedes* mosquitoes lay eggs on (κ^{Aedes}, denoted as κ^{Aedes} in [15]); iii) the number of eggs laid per batch by adult female *Culex* and *Aedes* mosquitoes (b_C and b_A, respectively); iv) the maximum density of eggs in the water body for mosquitoes to lay eggs (ρ_C and ρ_A, respectively, for *Culex* and *Aedes*).

Sobol sensitivity analysis

The Sobol method of sensitivity analysis quantifies the proportion of variance in a model output attributable to a specific parameter [21, 22]. A lower sensitivity index indicates that the parameter contributes minimally to output variations, whereas a higher sensitivity index signifies a greater influence on model variability. When a parameter has a low sensitivity index, rough estimations may be sufficient, whereas high-sensitivity parameters require more accurate estimation.

To conduct a Sobol sensitivity analysis, the first step is to define the parameter ranges and their probability distributions based on values reported in the current literature. Next, parameter sample sets are generated using quasi-random (i.e., deterministically generated values that achieve a more uniform space-filling distribution) sampling methods to ensure comprehensive coverage of the parameter space [17]. The model is then run repeatedly, resampling from these parameter sets to capture variations in the output. The model is run for eleven years, with the first ten years treated as an initial stabilization period to ensure system equilibrium under both constant and periodic parameter conditions; only outputs from the final year are used for sensitivity analysis. Finally, Sobol sensitivity indices are calculated.

These indices can be broken down into two key components: first-order indices and total-effect indices. The first-order indices represent the direct contribution of each parameter to the output variance, indicating how much influence a single parameter has when considered independently. In contrast, the total-effect indices account for both the direct effects and any interactions with other parameters, providing a more comprehensive view of how each parameter, including its interactions, influences the model's behavior. For example, if temperature has the highest first-order Sobol index, it suggests that it is a strong independent driver of the system. In contrast, if rainfall

exhibits a high total-order index but a low first-order index, this indicates that its influence arises mainly through interactions with other variables, such as vegetation. Meanwhile, if host availability has a very low Sobol index, it may not be a significant factor in the system, at least under the current assumptions.

The reliability and convergence of the Sobol indices is heavily dependent on the number of sample runs. The higher the number of samples, the more likely it is that the indices will converge on the 'true' value. However, the more samples run, the higher the computational cost and time taken. A commonly referenced approach to choosing the number of sample runs suggests that the total number of model evaluations should be proportional to the number of input parameters (D) plus two, multiplied by the number of baseline samples per parameter (N), following the formula $N \times (D + 2)$, where N is equal to one thousand [17]. We chose $N = 1500$, to ensure the Sobol indices are within the interval zero and one, and we found that on average, it took 33 minutes to complete a *Culex* scenario and 60 minutes to complete an *Aedes* scenario on R [23].

First order indices

Let the parameter of interest be Q_i, for $i = 1, \ldots, N$, where N is the number of parameters, Y is the outcome of the model which depends on the parameters Q_i (for instance, Q_1 is air temperature, Q_2 is water-bodies surface and Y is the total abundance of mosquitoes over one season). The first-order Sobol sensitivity index S_i quantifies the proportion of the total variance in the model output that is attributable solely to the variation in Q_i, while all other parameters are allowed to vary. In other words, it measures the reduction in model output variance if Q_i were fixed, leaving the other parameters to vary freely. The first-order Sobol index for a parameter Q_i is defined as the ratio of the variance of the conditional expectation $V(E[Y \mid Q_i])$ to the total output variance $V[Y]$, i.e,

$$S_i = \frac{V[E[Y \mid Q_i]]}{V[Y]}. \tag{3}$$

Here, $E[Y \mid Q_i]$ represents the expected value of the model output when Q_i is fixed and all other parameters are allowed to vary according to their distributions. Although the model used in this study is deterministic (i.e. it produces a single, fixed output for any given set of input parameters) Sobol sensitivity analysis treats the input parameters as random variables drawn from specified probability distributions. In practice, this conditional expectation is estimated through Monte Carlo sampling: for each fixed value of Q_i, multiple values of the remaining parameters are sampled, the model is evaluated for each parameter set, and the outputs are averaged. Repeating this process across the range of Q_i values allows for estimating the variance of $E[Y \mid Q_i]$, which, when normalized by the total output variance, yields the first-order Sobol index. The first-order index thus provides a measure of how much Q_i alone influences the overall variance in the model output.

Total effect indices

Letting the parameter of interest again be Q_i. The total effect Sobol sensitivity index T_i represents the proportion of variance in the model output that is attributable to Q_i, including both its direct contribution and all interactions with other parameters. It quantifies how much of the output variance would remain if all parameters except Q_i were fixed. In other words, it measures the total influence of Q_i, encompassing its individual effect and its combined effects with other parameters. The index is defined as,

$$T_i = 1 - \frac{V[E[Y \mid Q_{\sim i}]]}{V[Y]}, \tag{4}$$

where $Q_{\sim i}$ denotes all parameters except Q_i. Here, $E[Y \mid Q_{\sim i}]$ is the expected model output when all parameters other than Q_i are fixed and Q_i is allowed to vary. The variance $V[E[Y \mid Q_{\sim i}]]$ therefore reflects the remaining variability when Q_i is the only source of uncertainty. Subtracting this from the total variance $V[Y]$ yields the total contribution of Q_i to the output variance. The total effect index is especially useful for identifying parameters whose importance arises mainly through interactions, even if their individual (first-order) effects are small.

Results

The results are split into two subsections: the results of the literature review that will determine the parameter range, and the results of the sensitivity analysis.

Literature review

The differential equation systems describing the population dynamics of *Culex* (supplementary material [15]; Equation (1)) and *Aedes* (supplementary material [15]; Equation (2)) mosquitoes, model transitions through life stages including eggs, larvae, pupae, and three adult stages (nulliparous, i.e. females who have not laid eggs, flyers, i.e. females searching for oviposition sites, and parous, i.e. females who have laid eggs). While both species follow a similar structure, the *Aedes* model distinguishes between immature and mature egg compartments to capture additional detail in early development.

The key ecological parameters of interest are nested within equations, such that the area scanned by flyers ($\mathcal{A}$) appears in equations governing oviposition rate (η, supplementary material Equation (3)), the density of eggs per unit area (ρ) and the proportion of area that eggs are laid on (κ) appear in the equations governing the carrying capacity (K, supplementary material Eq (5) and (9)), and the number of eggs per batch (b) appear in the supplementary material Eq (6) and (10).

Within this section, we review the current literature split by parameter choice.

Typical area scanned by flyers

Understanding the typical area scanned (denoted by $\mathcal{A}$ in the model) by female mosquitoes, or 'flyers', in search of oviposition sites is crucial for predicting mosquito dispersal patterns and assessing the spread of mosquito-borne diseases. The term 'flyer' in this context refers to a female mosquito that has consumed a blood meal and is searching for a suitable site to lay her eggs. While the primary focus is on the distance travelled by females seeking oviposition sites, various approaches have been employed to estimate the general dispersal distance (i.e. the distance that a mosquito moves from point of origin to where they are found later) of mosquitoes, including isotope labelling and genetic techniques, which provide baseline estimates for dispersal behavior.

The initial estimation in [15] for the typical area scanned by flyers was based on the linear regression analysis conducted by Diallo et al. (2011) [24]. They predicted that people and livestock could be protected if they lived more than 1500 m to the nearest ponds due to the linear regression suggesting that mosquitoes would not disperse further than that distance. Lo Iacono et al. [15] used this distance for the diameter of the area spanned, however, going forward we will use the recorded dispersals as the radius for the area scanned.

Medeiros et al. (2017) [25] studied mosquito dispersal using isotope enrichment, revealing that 59% of *Culex quinquefasciatus* oviposition-site seeking females travelled

between 1-2 km from their larval habitat. In contrast, 79% of oviposition-site seeking *Aedes albopictus* females stayed within 250 m.

Ciota et al. (2012) [26] found that, among *Culex pipiens* and *Culex salinarius*, the mean distance travelled was 1.33 km. However, this study did not specifically focus on females searching for oviposition sites.

Linthicum (1985) [27] conducted an experiment in Kenya where a dambo was artificially flooded, leading to the emergence of *Aedes lineatopennis*. The mean dispersal distance for females of this species was 150 m.

Moore and Brown (2022) [28] reviewed the available data on the flight range of *Aedes aegypti* and concluded that the average flight distance for this species is 106 m. Another study of *Aedes aegypti* [29] found a mean dispersal distance of 45.2 m, with the distribution being Laplacian. This dispersal kernel (a probability distribution describing the likelihood of a mosquito being detected at various distances from its release point, regardless of the direction) was derived using a methodology that involved capturing adult female mosquitoes across high-rise apartment blocks with simple oviposition traps. The study reported that there is a 50% probability of effective dispersal occurring within 32 m and a 10% probability of flight extending beyond 100 m. This research used genetic techniques to identify closely related kin and the distances between them.

Verdonschot et al. (2014) [30] conducted a thorough review of mark-recapture experiments across the *Aedes* genera and reported an average flight distance of 89 m for *Aedes* mosquitoes and 609.5 m for *Culex* mosquitoes. The review also highlighted the maximum flight distances: 2959 m for 24 species of *Aedes* mosquitoes and 5014 m for 13 species of *Culex* mosquitoes.

The values reported by Medeiros et al. (2017) [25] are particularly relevant for our analysis, as they specifically refer to oviposition-seeking *Culex* females. The authors also provide a graph depicting the distribution of dispersal distances (see [25]; Fig 10B), which aligns with a triangular distribution. Although the values are given in terms of radius, we can convert them to an area by calculating the area of a circle with the corresponding radius. For a triangular distribution, we require minimum, maximum, and mode values. Based on the data, the minimum area is 0.196 km^2 (radius 0.25 km), the maximum area is 15.904 km^2 (radius 2.25 km), and the mode area is approximately 9.621 km^2 (radius 1.75 km).

For *Aedes* flyer flight range, based on the data available, we have selected a gamma distribution with shape 2.5 and scale 10000. See S1 Table for summary of results and S1 Appendix for the method to estimate this distribution.

Proportion of water body area/soil in which eggs are laid

The proportion of the water body area or soil in which eggs are laid, denoted as κ in the model, is an important parameter for understanding mosquito oviposition behavior. Soti et al (2012) [31] indicates that the inner distance from the pond border defining the laying area of Culex on the water is about 1m. However, in general, there is a notable lack of specific empirical data on this parameter for both *Aedes* and *Culex* species. Consequently, due to the absence of concrete evidence, we apply a wide range of values for κ spanning from 0.001 to 0.999, distributed uniformly, for both species.

Number of eggs per batch

The oviposition strategies of *Aedes* and *Culex* mosquitoes differ significantly. *Culex* mosquitoes typically lay their eggs in cohesive rafts on the water surface, whereas *Aedes* mosquitoes deposit desiccation-resistant eggs singly on moist surfaces, allowing them to withstand dry conditions until favorable hatching conditions arise [32]. The number of

eggs laid per batch, b, which are in general different, has been explored in various studies.

Several studies have quantified egg production within the *Culex* genus. In *Culex pipiens molestus*, females deprived of a blood meal produced an average of 37 eggs per raft [33]. In contrast, blood-fed *Culex pipiens pallens* laid an average of 85.12 ± 2.07 eggs per raft [34]. Notably, *Culex pipiens pipiens* captured from the wild produced significantly more eggs, averaging 213.9 ± 8.7 per raft [35]. The number of eggs laid also varied with blood source: *Culex pipiens* fed on human, rabbit, and pigeon blood produced rafts containing 161.3 ± 6.4, 102.2 ± 5.8, and 146.1 ± 4.7 eggs, respectively, with an overall range of 68 to 188 [36]. Similarly, *Culex pipiens* females fed on live quail blood produced an average of 199.89 ± 7.24 eggs per raft [37], while *Culex quinquefasciatus* fed on chicken blood laid between 125 and 140 eggs per raft [38]. Age can also influence fecundity in Culex quinquefasciatus, with egg production per raft ranging from 43 to 231 eggs across individuals of different ages. Although fecundity generally declined as mosquitoes aged, the mean number of eggs per raft remained high at 152.9 ± 43.4 eggs [39]. Surprisingly, sugar-deprived *Culex quinquefasciatus* females produced a similar number of eggs per raft (210 ± 12) compared to sugar-fed females (200 ± 10) [40].

In contrast, fewer studies have documented the egg production of *Aedes* mosquitoes. However, available data allow for reasonable estimation of oviposition parameters. *Aedes aegypti* females fed on human, rabbit, and pigeon blood laid an average of 50.4 ± 2.7, 33.2 ± 1.8, and 46.3 ± 3.6 eggs per batch, respectively, with an overall range of 22 to 83 eggs [36]. Similarly, another study reported that *Aedes aegypti* females fed on rabbit blood produced 35 to 40 eggs per gonotrophic cycle [38]. Zeller and Koella [41] found that *Aedes aegypti* reared on a high amount of food throughout development laid the most eggs (67 ± 8.1), while those switched from high to low food produced the fewest (31 ± 5.2) (see [41]; Figure 3C). Both the likelihood of laying eggs and the total number of eggs were strongly influenced by the food available during late development. Pedreira Padilha et al. [42] found that in the second and third gonotrophic cycles, *Aedes aegypti* females laid approximately 70 eggs per batch. Furthermore, Yan et al. [43] explored the effects of nutritional status on fecundity and reported that well-nourished *Aedes aegypti* females laid an average of 90 eggs per batch, with a range of approximately 60 to 125 eggs.

Synthesizing this information, we propose that the number of eggs per batch in *Culex* mosquitoes follows a normal distribution with a mean of 149 and a standard deviation of 16.2. For *Aedes* mosquitoes, the best fit is a normal distribution with a mean of 55 and a standard deviation of 2.80, aligning with the observed fecundity ranges reported in the literature. See S1 Appendix for the method to estimate these distributions.

Maximum surface density of eggs

Despite numerous studies on mosquito oviposition behavior, direct estimates of the maximum surface density of mosquito eggs ρ (i.e., the number of eggs per unit area) were not returned from the scoping review. While some research has explored how female mosquitoes respond to existing eggs or larvae when selecting oviposition sites, these studies do not explicitly quantify maximum egg densities. Consequently, any estimates must be inferred from indirect evidence, and a broad parameter range is necessary to reflect this uncertainty.

For *Culex* mosquitoes, an informative study by Shin et al. (2019) [44] investigated oviposition preferences in water containers with varying surface areas available for egg-laying. The authors noted that the highest number of egg rafts retrieved at once were 34, 164, and 32 for *Culex coronator*, *Culex nigripalpus*, and *Culex quinquefasciatus*, respectively, summing to a total of 230 egg rafts. Using our previously determined

average of 150 eggs per raft, this yields an estimate of 34 500 eggs in a $0.06\,\mathrm{m}^2$ (approximately a circular area of 14 cm radius) water body, equating to an approximate density of 575 000 eggs per m^2.

A second study investigated how the presence of varying numbers of pre-existing Culex egg rafts influenced subsequent oviposition behavior [45]. The experiment included a range of egg raft quantities, with the highest treatment containing up to 100 egg rafts. Since converting these volumes to surface densities is challenging, and due to the absence of definitive data on a biologically constrained maximum density, we adopt a conservative uniform distribution for this parameter, ranging from 500 000 to 20 000 000 eggs per m^2, based on findings from both studies.

For *Aedes* mosquitoes, fewer studies provide insight into egg density. One study, aimed at improving *Aedes albopictus* ovitraps, recorded a maximum egg density of 0.49 eggs per cm^2, equivalent to $4.90\ 10^3$ eggs per m^2 [46]. While this may not reflect the absolute maximum, it provides a useful lower bound for estimation. Another study investigating the distribution of *Aedes caspius* and *Aedes vexans* eggs among different vegetation types in Poland found that the highest egg densities, recorded in perennial nitrophilous plant communities, averaged 450.52 ± 227.99 eggs per $400\,\mathrm{cm}^2$ [47]. This translates to an average density of approximately $1.125\ 10^4$ eggs per m^2, with an upper estimate (including standard error) of about 15 675 eggs per m^2.

Given the significant disparity between the estimated maximum densities for *Culex* and *Aedes* mosquitoes, spanning several orders of magnitude, it is reasonable to expect that *Aedes* egg density is inherently lower due to their oviposition strategy. Unlike *Culex* mosquitoes, which lay tightly packed egg rafts, *Aedes* species deposit their eggs singly, often over dispersed surfaces [48]. However, the lack of direct studies quantifying maximum egg densities for *Aedes* introduces considerable uncertainty. To account for this, we adopt a conservative approach by applying a broad uniform distribution, ranging from 12 000 to 1 000 000 eggs per m^2, ensuring that the full plausible range is considered.

Parameter choice

Table 2 provides a comprehensive summary of the parameter ranges and distributions derived from the literature reviewed in the preceding sections. Each parameter, representing key aspects of mosquito dispersal and oviposition behavior, has been assigned an appropriate statistical distribution based on available empirical data or, where data is scarce, a conservative assumption. For dispersal area ($\mathcal{A}$), triangular and gamma distributions were chosen to reflect the observed variability in flight range. The proportion of water body or soil utilized for egg-laying (κ) is represented by a uniform distribution, due to the absence of direct evidence. The number of eggs per batch (b) follows a normal distribution, with species-specific means and standard deviations informed by multiple studies. Finally, the maximum surface density of eggs (ρ) is modelled using a uniform distribution, reflecting the uncertainty in available estimates. This table consolidates all relevant parameter choices, ensuring a structured approach to model formulation.

Table 2. Parameter range and distribution summary.

Parameter	Symbol and Dimension	Distribution	Values	Rationale
Area scanned by *Culex* looking for oviposition sites	$\mathcal{A}_C$ [L^2]	Triangular	Min = 196 000 m^2, Max = 15 904 000 m^2, Mode = 9 621 000 m^2	[25]
Area scanned by *Aedes* looking for oviposition sites	$\mathcal{A}_A$ [L^2]	Gamma	Shape = 2.5, Scale = 10 000	[25, 27–30]
Proportion of the water body area that eggs are laid on	κ^{Culex} [-]	Uniform	Min = 0.001, Max = 0.999	Arbitrary
Proportion of area on the soil where eggs are laid on	κ^{Aedes} [-]	Uniform	Min = 0.001, Max = 0.999	Arbitrary
Number of eggs laid per batch by *Culex*	b_C [-]	Normal	Mean = 149, SD = 16.2	[33–40]
Number of eggs laid per batch by *Aedes*	b_A [-]	Normal	Mean = 55, SD = 2.80	[36, 38, 42, 43]
Eggs maximum density per m^2	ρ_C [L^{-2}]	Uniform	Min = 500000, Max = 20000000	[44, 45]
Eggs maximum density per m^2	ρ_A [L^{-2}]	Uniform	Min = 12000, Max = 1000000	[46, 47]

Sensitivity analysis

Culex sensitivity analysis

The overall results with fixed values of temperature, water body area, and detection probability all assigned to medium (Fig 1), indicate that of the four parameters of interest, the most influential, in descending order, are the area scanned when looking for oviposition sites ($\mathcal{A}_C$), the proportion of the water body area where *Culex* lay their eggs (κ^{Culex}), the eggs maximum density per m^2 (ρ_C), and the number of eggs laid per batch (b_C).

Looking individually at temperature, water body area, and detection probability sheds some light on what causes a change in how influential the parameters are on the model output (Fig 2).

The analysis of the variation in indices between $21°C$ and $29°C$ reveals notable trends for both first-order indices and total effect indices (Fig 2A). For the first-order indices of $\mathcal{A}_C$, there was a decrease of 20% between $21°C$ and $25°C$, followed by a smaller decline of 3% between $25°C$ and $29°C$. In terms of the total effect indices of $\mathcal{A}_C$, a 21% decrease was observed between $21°C$ and $25°C$, with a 4% decrease from $25°C$ to $29°C$. Additionally, κ^{Culex} cumulatively increased 2.3 times and ρ_C increased 2.4 times for first-order indices and a 21% and 23% increase in both the total effect indices, respectively. No significant changes were observed in the number of eggs laid per batch.

The analysis of the variation in indices between $10\,000\,m^2$ and $25\,000\,m^2$ reveals notable trends for both first-order indices and total effect indices (Fig 2B). As the water body area increases, the relative importance of κ^{Culex} and ρ_C increases to approximately 6.9 times and 9.0 times their original values, respectively, for first-order indices, and to about 1.8 times and 1.9 times their original values, respectively, for total effect indices. Notably, the area scanned decreases in importance as the water body increases, dropping to about one-third of its original value for both first-order and total effect indices, with its importance notably reduced when the water body area reaches $25\,000\,m^2$. Further, there are no notable changes in the number of eggs laid per batch.

As the value of detection probability increases, the relative importance of all parameters stays level (Fig 2C). However, the importance of κ^{Culex} and ρ_C swap order when considering first order indices and total effect indices.

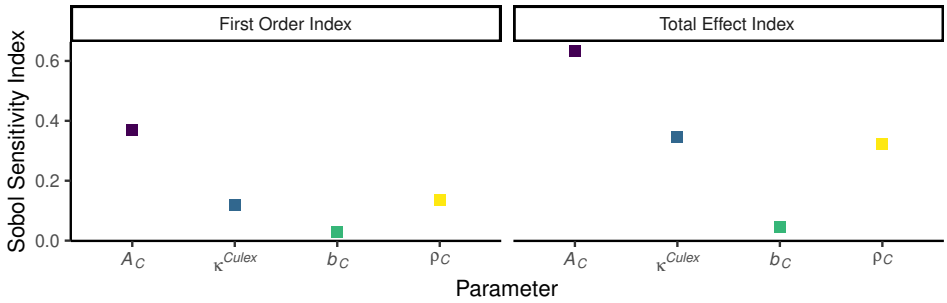

Fig 1. First order and total effect Sobol sensitivity indices for *Culex* mosquitoes. With medium values of temperature, water body area and detection probability.

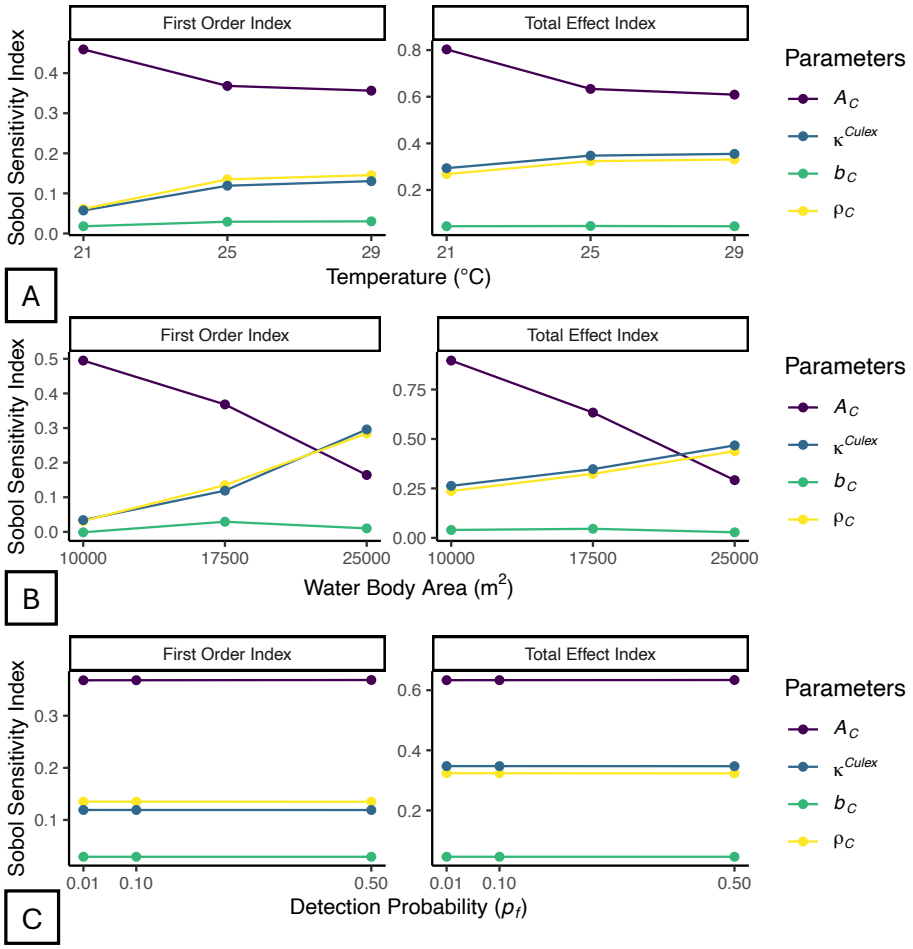

Fig 2. Sobol sensitivity indices for *Culex*. Comparing varying values of constant: temperature, water body areas, and detection probabilities.

Aedes sensitivity analysis

The same set of analyses were repeated for the equivalent *Aedes* model. The overall results, where medium values of temperature, water body area, and detection probability were used, show that, the proportion of water body where eggs are laid κ^{Aedes} was the most influential parameter (Fig 3). The remaining three parameters had a different order of importance to that seen in the *Culex* analysis, with the second most influential parameter being ρ_A, the third being $\mathcal{A}_A$, and the least important, again, being b_A.

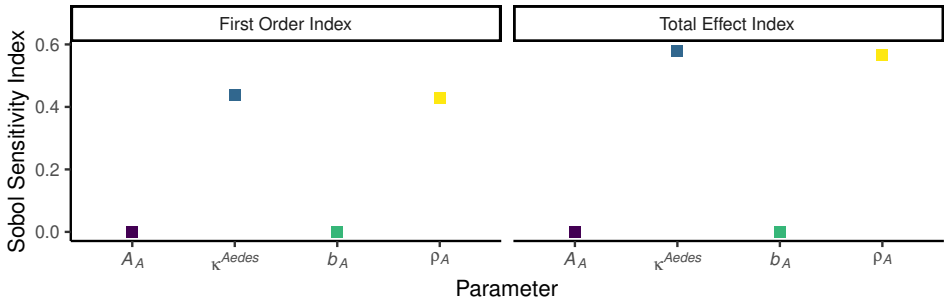

Fig 3. First order and total effect Sobol sensitivity indices for *Aedes* mosquitoes. With medium values of temperature, water body area and detection probability.

Looking individually at temperature, water body area, and detection probability reveals no notable trends for both first-order indices and total effect indices (S1 Fig). The order of importance and the index remains relatively constant throughout.

Periodic temperature and water body

Running the analysis again with periodic functions for temperature (Eq (1)) and water bodies (Eq (2)), we obtain S2 Fig. It can be observed that the order of the indices does not change when compared to the analysis with medium constant temperature, water body and detection probability. Additionally, the values of for the *Aedes* simulation remain relatively the same, whilst we observe some minor changes for the *Culex* indices. When we change the periodic functions to be out of phase, we obtain the same order of results.

Discussion and conclusion

This study aimed to clarify the ecological drivers of mosquito population dynamics that underpin the transmission of Rift Valley fever virus (RVFV), with a particular focus on vector ecology. A deterministic, compartmental ecoepidemiological model of RVFV transmission was used to capture the interactions between mosquito life cycles, environmental conditions, and disease spread. However, several key ecological parameters in the model, such as those governing oviposition and the carrying capacity, remain poorly constrained by empirical data, introducing uncertainty into model predictions. To address this, we conducted a sensitivity analysis to quantify the relative influence of these uncertain parameters on mosquito abundance. By identifying which parameters most strongly affect model outcomes, our goal is to guide future data collection efforts and improve the reliability of model-based assessments for RVFV risk and control.

The scoping review highlights a scarcity of research in some areas. For instance, while the literature contains numerous references to mosquito egg production, much of

this research is laboratory-based and often features experimental variables being tested (such as diet) that make the numbers difficult to generalize to field scale. Furthermore, the numbers also vary considerably within and between species (see Table 2). We found far fewer articles referring to egg production of *Aedes* mosquitoes than *Culex* mosquitoes. Furthermore, all *Aedes* studies described here focus on a single species: *Aedes aegypti*.

In addition, we found a similar dearth of studies observing the density of mosquito eggs in the field (or, indeed, in the laboratory). Most significantly, based on our scoping review, we note an absence of research into spatial oviposition dynamics across water bodies. For *Aedes* mosquitoes, our particular measure of interest refers to the area of the ring of damp soil around the water body in which eggs are laid, divided by the area of the water body itself, whereas for *Culex* mosquitoes this refers to the actual surface area of water across which eggs are laid divided by the area of the whole water body. While we could not gather any information from the literature to influence our specific parameter estimates, it is important to state that we were unable to find any data regarding patterns of mosquito egg laying across water bodies.

Since the model is set up to read empirical data for air temperature, water body area and livestock numbers, we initially chose to set these as constants to allow for a more transparent analysis. This approach helps isolate the influence of other parameters and ensures that any observed sensitivity in the Sobol analysis is not confounded by fluctuations in these environmental inputs. However, a major limitation for this is that the model for *Aedes* relies on the fluctuation of the water body for the hatching of the mature eggs to larvae, an important mechanism that is suppressed when water availability is fixed. To address this, we also repeated the analysis using periodically varying temperature and water body area, based on Eq. (1)-(2), which more realistically capture seasonal dynamics and enable the emergence of key temporal patterns in mosquito population behavior. Nevertheless, the analysis was firstly conducted with the three levels of constant temperature, water body area, and also the probability of a mosquito detecting livestock (p_f in the model). Regarding this parameter, it should be noted that, by construction, the density-dependent model for the number of eggs per batch (Eq (6) and (10) in the supplementary material of [15]) is only valid when the vector-to-host ratio, and therefore the parameter p_f, is strictly greater than zero.

We chose to utilize Sobol sequences to generate our parameter sample sets due to their proven advantages in sensitivity analyses. Compared to Latin Hypercube Sampling (LHS) and random sampling, Sobol sequences have been shown to result in faster convergence, lower computational cost, and improved reproducibility [49]. This method ensures that the parameter space is sampled more uniformly, which is critical for reliable sensitivity analysis.

The sensitivity analysis showed that the area scanned by *Culex* is the most sensitive, in contrast to the situation for *Aedes* which exhibits a very low Sobol sensitivity index. This is irrespective of the temperature, probability of detection and in part for water bodies. However, when comparing the maximum proportions of scanned area (based on the distributions) that is actual water (based on the medium value for water bodies), we observe that 17% of the area scanned for *Aedes* is water, and for *Culex* it is 0.11%. This may give an indication of why the parameter $\mathcal{A}_A$ is not critical in the model.

The analysis also showed that in both populations the indexes for the eggs maximum density and the proportion of area of the water body/soil where mosquitoes lay their eggs have similar value. This is expected because both parameters only affect the carrying capacity for eggs and the minimal differences are expected due to only the ranges of the chosen values.

For both models, the number of eggs laid is among the least sensitive parameters. The ranges observed in the literature, 106.7 eggs for Culex and 18.5 eggs for Aedes, reflect differences due to species, feeding status, and experimental conditions. However,

the sensitivity analysis suggests that even across this biologically realistic range, the impact on the overall model output is minimal. This indicates that variability in egg production due to factors such as whether mosquitoes are blood-fed or the specific species used is unlikely to significantly influence model predictions. Therefore, any value within the reported range can be considered suitable for use in the model without substantially affecting its robustness.

According to our sensitivity analysis, in both populations, changing the value of the probability of a mosquito detecting livestock has no impact on the relative importance of the indices. In the current model with no disease, this probability merely rescales the vector-to-host ratio by a constant factor ($\mathrm{p_f}$). The vector-to-host ratio, in turn, influences the density-dependent number of eggs per batch and the biting rate (Eq. (6), (10), (13), and (20) in [15] based on [50]. However, this effect is negligible under the current model, which assumes that host density only becomes impactful when the number of hosts is extremely low compared to the number of vectors (mathematically, this is because the parameter $q = 10^{11}$ in [15] approaches infinity, where q represents the vector-to-host ratio at which vector fecundity is halved). This factor is expected to become important however, when the low number of hosts limits blood meal significantly reducing the number of eggs per batch and the biting rate. The vector-to-host ratio is also expected to be important in an epidemiological situation as this affects the force of infection.

When considering the changes in temperature in the *Culex* population (Fig 2A), the results suggest that the indices are more sensitive to temperature changes between 21°C and 25°C, with a slower decline observed beyond 25°C. Since temperature is incorporated into the development rates and mortality rates (see S3 Appendix), then it is not obvious how temperature influences the changes highlighted in the observations.

On the other hand, when considering the water body area, the parameters do not uniformly become more or less sensitive to changes. It is observed that the area scanned, $\mathcal{A}_C$, loses sensitivity, while others parameters (the proportion of water body area they lay eggs on, κ^{Culex}, and maximum density of eggs in the water body, (ρ_C)) gain it. A possible explanation for this is the structure of the equations themselves: as seen in [15] supplementary information, Eq. (3), the influence of $\mathcal{A}_C$ is relative to the oviposition rate, so an increase in water surface area diminishes the effect of $\mathcal{A}_C$. Hence, we observe a loss in sensitivity. Meanwhile, Eq. (5) shows that increases in water body area directly amplifies the carrying capacity (with the equation becoming more sensitive to changes in ρ or κ), which then feeds into Eq. (4), increasing the variance in the number of eggs laid. Therefore, as water body area expands, parameters like ρ and κ exert a stronger influence on the system, while parameters like $\mathcal{A}_C$, which scale with water body area, become less impactful.

In comparison, when studying the *Aedes* model, we find the most sensitive parameters throughout the analysis are the proportion of water body they lay eggs on (κ^{Aedes}) and the maximum density of eggs in the water body (ρ). This is likely due to the interaction of the two parameters in Eq. (9) [15], as before. Yet, in this analysis, we did not see changes in any other parameter when we changed the temperature, water body area or the detection probability.

To better understand the source of the observed sensitivity patterns, we conducted an additional analysis in which the Sobol sampling matrices generated for one mosquito system were applied to the other (see S4 Appendix). Specifically, the matrices created for the *Aedes* model were used in the *Culex* model, and vice versa. We found that each system returned sensitivity indices that closely resembled those from the original model associated with the Sobol matrix. For example, applying the *Aedes* Sobol matrices to the *Culex* model produced results similar to those obtained in the *Aedes* model. This indicates that the sensitivity patterns are primarily driven by the parameter ranges and

distributions used in the Sobol sampling, rather than by differences in the mosquito system structure itself.

Extending the analysis, we incorporated fluctuating temperature and water body values using periodic functions, following the approach in [15]. Although one might expect these fluctuations to obscure the effects of individual parameters, the sensitivity results reveal that the order of the Sobol indices remains consistent with those obtained under constant medium values. This consistency suggests that the model's behavior is stable under both static and dynamic environmental conditions, and further confirms that the relative influence of each parameter is robust and not significantly altered by environmental variability.

Given the robustness of the model across both constant and fluctuating environmental conditions, attention should now shift toward refining key ecological assumptions that influence oviposition behavior. In particular, there is a need to allocate research resources toward better understanding the proportion of the water body area or soil that female adult mosquitoes actually use for laying eggs. Closely related is the need to quantify the maximum egg density that a water body can support before it deters further oviposition. Additionally, gaining insight into the typical area scanned by flying *Culex* mosquitoes when searching for suitable oviposition sites would significantly improve the spatial realism of the model. Addressing these gaps would allow for more accurate representation of mosquito population dynamics, especially in heterogeneous or resource-limited environments, and enhance the predictive power of vector-borne disease models.

Supporting information

S1 Table. Summary of literature search for the typical area scanned by flyers.

S1 Fig. Sobol sensitivity indices for *Aedes*. Comparing varying values of constant: temperature, water body areas, and detection probabilities.

S2 Fig. Sobol sensitivity indices with in-phase periodic functions for temperature and water bodies. A: *Culex*. B: *Aedes*.

S1 Appendix. Calculation of Distributions.

S2 Appendix. Parameters. Input parameters for the model.

S3 Appendix. Investigation into parameters. Investigating the impact of development rate, mortality rate and oviposition rate when there is constant temperature and water body.

S4 Appendix. Investigation into differences. Using the same Sobol matrices, we put them in the opposite mosquito system to observe any differences.

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