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Mathematical modelling of mosquito dispersal in a heterogeneous environment

Angelina Mageni Lutambi [a,b,c,*], Melissa A. Penny [a,b], Thomas Smith [a,b], Nakul Chitnis [a,b]

[a] Swiss Tropical and Public Health Institute, Socinstrasse 57, P.O. Box CH-4002 Basel, Switzerland
[b] University of Basel, Petersplatz 1, CH-4003 Basel, Switzerland
[c] Ifakara Health Institute (IHI), Plot 463, Kiko Avenue, Old Bagamoyo Road, Mikocheni P.O. Box 78373, Dar es Salaam, Tanzania

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ABSTRACT

Mosquito dispersal is a key behavioural factor that affects the persistence and resurgence of several vector-borne diseases. Spatial heterogeneity of mosquito resources, such as hosts and breeding sites, affects mosquito dispersal behaviour and consequently affects mosquito population structures, human exposure to vectors, and the ability to control disease transmission. In this paper, we develop and simulate a discrete-space continuous-time mathematical model to investigate the impact of dispersal and heterogeneous distribution of resources on the distribution and dynamics of mosquito populations. We build an ordinary differential equation model of the mosquito life cycle and replicate it across a hexagonal grid (multi-patch system) that represents two-dimensional space. We use the model to estimate mosquito dispersal distances and to evaluate the effect of spatial repellents as a vector control strategy. We find evidence of association between heterogeneity, dispersal, spatial distribution of resources, and mosquito population dynamics. Random distribution of repellents reduces the distance moved by mosquitoes, offering a promising strategy for disease control.

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1. Introduction

Mosquitoes transmit malaria, dengue, yellow fever, filariasis, and several other important diseases. Malaria, in particular, shows considerable spatial variation predominantly determined by climatic variation [25], intervention coverage, and human movement [39,55,60,62]. At local scales (i.e. from 100 m to 1 km), mosquito behaviour and ecology play an important role in determining the distribution of transmission [34]. Like other animals, mosquitoes can move in any direction, motivated by resource availability and other drivers of dispersal, but can only travel over limited distances. Control interventions should consider locality and mosquitoes' ability to move, to achieve a high level of effectiveness in reducing the mosquito population.

The impact of vector dispersal in the spread and control of diseases was first highlighted a century ago by Ronald Ross [53], but has received limited attention within the public health community. Ross stipulated that mosquito density within any area is always a function of four variables, which include the reproduction rate, mortality rate, immigration, and emigration rates. A study by Manga et al. [38] also showed that the spatial variation in the distribution of resources used by mosquitoes affects their reproduction and their rate of dispersal. This in turn contributes to variation in densities [10,24,37,58], human exposure to vectors, and the ability to control disease transmission [55]. The effects of resource availability on transmission can be surprising. For instance, even the presence of non-productive larval habitats may affect biting densities [34]. However, conducting experimental studies of mosquito dispersal [21–23,42] are challenging.

Mathematical models play an important role in understanding and providing solutions to phenomena which are difficult to measure in the field, but few models have incorporated dispersal or heterogeneity when modelling resource availability [17,34,46,49,58,68] or varied the usual assumption of a closed vector population [45,50,67]. Others have sub-divided the adult stage of the mosquitoes into different stages [45,50,54]. To investigate the effects of dispersal and heterogeneity, a model should incorporate features of the mosquito life cycle, the feeding cycle, spatial heterogeneity in mosquito resources, and dispersal.

Spatial models have commonly used the diffusion approach, which considers space as a continuous variable. Despite the existence of diffusion models, which account for heterogeneity [51,63], it is difficult to explicitly incorporate the various factors that affect movement. For example, in areas where resources are located in patches or discrete locations, mosquito dispersal is more conveniently modelled using a metapopulation approach, in which the population is divided into discrete patches. In each patch, the

* Corresponding author at: Swiss Tropical and Public Health Institute, Socinstrasse 57, P.O. Box CH-4002 Basel, Switzerland. Tel.: +41 612848273; fax: +41 612848101.

E-mail addresses: angelina-m.lutambi@unibas.ch (A.M. Lutambi), melissa.penny@unibas.ch (M.A. Penny), thomas-a.smith@unibas.ch (T. Smith), Nakul.Chitnis@unibas.ch (N. Chitnis).

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population is sub-divided into subgroups, corresponding to different states, leading to a multi-patch, multi-compartment system.

Several models using diffusion approaches [18,19] have incorporated heterogeneity and have shown that the environment has a strong influence on the distribution of disease vectors. However, none of them have included the aquatic stages of the mosquitoes or have provided a general and simple framework for modelling arbitrary spatial patterns of mosquito control interventions. A model framework that includes the aquatic stages and that partitions space into discrete locations allows us to capture the various forms of spatial heterogeneity that exist in our environment.

In this paper, a mathematical model, that includes all of the above features is developed and simulated to investigate the impact of dispersal and heterogeneous distribution of mosquito resources, such as hosts and breeding sites, on the spatial distribution, dynamics, and persistence of mosquito populations. The distance a mosquito can travel from its place of emergence or food source is a critical factor for vector control interventions, thus the model is used to project likely dispersal distances and considers how these might be changed by vector control interventions.

In the following sections, we develop and analyse a model for mosquito population dynamics that does not consider movement of mosquitoes. We then develop a meta-population model for mosquito movements with discrete space in hexagonal patches and compare it to a continuous space model. We then combine the two models and run simulations of a spatially explicit model of the full mosquito life cycle to determine the effect of repellents.

2. Description of the basic model: mosquito dynamics without dispersal

Mosquito life begins with eggs, which hatch into larvae under suitable conditions. The larvae develop into pupae that mature and emerge into adults (see Fig. 1). Female mosquitoes then feed on human or animal blood to provide protein for their eggs. After biting, female mosquitoes rest while their eggs develop. Once eggs are fully developed, the females oviposit and then proceed to find another blood meal thus completing the mosquito feeding cycle [12].

Ignoring the effects of hibernation and breaks in the reproductive cycle, and assuming that eggs deposited at breeding sites proceed through development immediately [56], we consider six compartments of the mosquito life cycle: eggs (E), larval (L), pupal (P), host seeking adults (A_h), resting adults (A_r), and oviposition site seeking adults (A_o) (Fig. 1). In contrast to other models [36], we distinguish all of these stages because interventions may be applied to any one (or more) of them. Since only female mosquitoes are involved in the transmission of vector-borne diseases, this model ignores males. The six subgroups have different mortality and progression rates. Each subgroup is affected by three processes: increase due to recruitment, decrease due to mortality, and development or progression of survivors into the next state. The parameter b is the average number of female eggs laid during an oviposition and ρ_{A_o} (day^{-1}) is the rate at which new eggs are oviposited (i.e. reproduction rate). Exit from the egg stage is either due to mortality, μ_E (day^{-1}), or hatching into larvae, ρ_E (day^{-1}). In the larval stage, individuals exit by death or progress to pupal stage at a rate, ρ_L (day^{-1}). Assuming a stable environment, inter-competition for food and other resources for larvae may occur, leading to density-dependent mortality, $\mu_{L_2}L^2$ (day^{-1} mosquitoes^{-1}) or natural death at an intrinsic rate, μ_{L_1} (day^{-1}). Pupae die at a rate, μ_P (day^{-1}) and survivors progress and emerge as adults at rate ρ_P (day^{-1}). In the adult stage, host seeking mosquitoes die at a rate μ_{A_h} (day^{-1}). Those surviving this stage, and if they are successful in feeding, enter the resting stage at a rate ρ_{A_h} (day^{-1}). In the resting stage, mosquitoes die at a rate, μ_{A_r} (day^{-1}). Survivors progress to the oviposition site searching stage at a rate ρ_{A_r} (day^{-1}). Oviposition site searchers die at rate μ_{A_o} (day^{-1}) and after laying eggs return to the host seeking stage. These processes account for the dynamics of each subgroup over time. Although mosquitoes might require more than one blood meal to produce eggs [5], this model assumes the simple case where only one blood meal is enough for eggs to mature. Throughout this work, we use the words oviposition sites and breeding sites interchangeably.

From the description above, we develop the following system of differential equations to describe mosquito dynamics without movement:

$$\begin{aligned}
\frac{dE}{dt} &= b\rho_{A_o}A_o - (\mu_E + \rho_E)E, \\
\frac{dL}{dt} &= \rho_E E - \left(\mu_{L_1} + \mu_{L_2}L + \rho_L\right)L, \\
\frac{dP}{dt} &= \rho_L L - (\mu_P + \rho_P)P, \\
\frac{dA_h}{dt} &= \rho_P P + \rho_{A_o}A_o - \left(\mu_{A_h} + \rho_{A_h}\right)A_h, \\
\frac{dA_r}{dt} &= \rho_{A_h}A_h - (\mu_{A_r} + \rho_{A_r})A_r, \\
\frac{dA_o}{dt} &= \rho_{A_r}A_r - (\mu_{A_o} + \rho_{A_o})A_o,
\end{aligned} \tag{1}$$

with initial conditions $E(0), L(0), P(0), A_h(0), A_r(0)$, and $A_o(0)$. Mosquito survival in each stage and the progression period from one stage to the next are assumed to be exponentially distributed. The definitions of state variables and the associated parameters are given in Tables 1 and 2, respectively.

Since the system in Eq. (1) monitors populations in each stage of mosquito development and because all model parameters (Table 2) are positive, there exists a region $\mathbb{D}$ such that

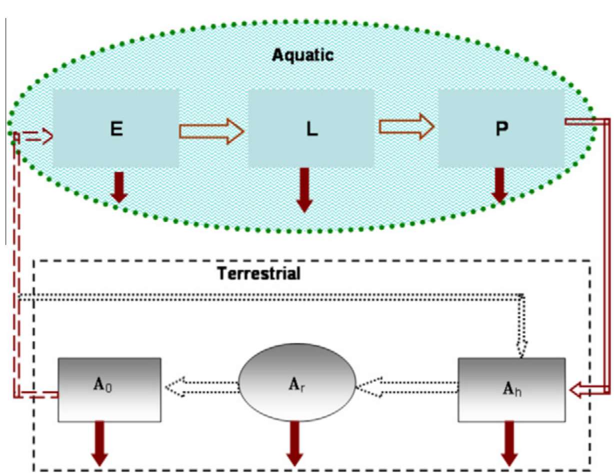

Fig. 1. Schematic representation of *Anopheles* mosquito life cycle and feeding cycle. Model states are Eggs (E), Larvae (L), Pupae (P), host seeking adults (A_h), resting adults (A_r), and oviposition site searching adults (A_o).

Table 1
State variable definitions.

Variable	Description
E	density of eggs
L	density of larvae
P	density of pupae
A_h	density of mosquitoes searching for hosts
A_r	density of resting mosquitoes
A_o	density of mosquitoes searching for oviposition sites

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