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A network population model of the dynamics and control of African malaria vectors

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Abstract

A more robust assessment of malaria control through mosquito larval habitat destruction will come from a better understanding of the distribution, productivity and connectivity of breeding sites. The present study examines the significance of vector dispersal ability, larval habitat stability and productivity on the persistence and extinction of a mosquito population inhabiting a dynamic network of breeding sites. We use this novel method of vector modelling to show that when dispersal is limited or vector distribution is patchy, the spread and growth of a mosquito population at the onset of a rainy season is delayed and extinction through larval habitat destruction is more readily achieved. We also determine the impact of two alternative dry-season survival strategies on mosquito dynamics. Simulations suggest that if adult vectors remain dormant throughout the dry season, the stage structure of the population will be synchronized at the onset of the wet season and its growth will be delayed. In contrast, a population that continues to breed throughout the dry season grows more rapidly and is more difficult to control. Our findings have important implications on the development of integrative malaria vector management strategies and on the understanding of dry-season survival mechanisms of African malaria vectors.

Keywords

Mosquito dispersal; habitat stability; vector dynamics; integrated vector management

Introduction

There has been a recent emphasis on integrating multiple vector management tools to strategically optimize malaria control programs.^{1,2} Fundamental to understanding vector ecology and management is an appreciation for the availability of mosquito breeding sites, and the impact that integrating larval and adult control programs can have on vector densities and disease epidemiology.^{3,4} The immature stages of *Anopheles gambiae*, the primary vector of human malaria in Africa, develop in aquatic environments generally consisting of small, often transient pools of water.^{5–7} Preference of gravid females to oviposit in proximal,^{8,9} unstable

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habitats and the resulting effects on population dynamics is an aspect of mosquito ecology that is generally ignored.^{10–13}

Despite the evidence that species persistence can be as much a factor of the connectivity within a metapopulation as the productivity of its constituent subpopulations,¹⁴ little attempt has been made to elucidate the significance of malaria vector dispersal in its abundance and control. Recently, Depinay et al. (2004) developed an individual based spatial model and attempted to describe the significance of anopheline larval habitat distribution and stability,¹⁵ however one important assumption in their models – unrestricted, random adult movement between resource sites – is an oversimplification. This issue was partly addressed by Gu et al. (2006) who tracked the movement of individual mosquitoes seeking out breeding sites.¹⁶ Their simulation on a two-dimensional lattice showed that habitat destruction as a control measure was approximately half as effective when a mosquito was twice as adept at locating oviposition sites.¹⁶ They suggest that neglecting to consider the mosquito's ability to locate oviposition sites might result in hundred-fold discrepancies in calculations of the basic reproductive number of malaria. Several other theoretical studies of malaria vector dynamics have also emphasized the importance of considering individual larval habitats, but not addressed the significance of interactions between larval habitat connectivity, stability and productivity.^{17–19}

Here we present a stochastic network population model to examine the significance of larval habitat connectivity, stability and productivity on the persistence of a mosquito population. The nodes of the network represent mosquito breeding sites that are connected by dispersing adults. *Anopheles gambiae* are endophagic, hence their feeding sites are static.²⁰ There is ample evidence to suggest that even in urbanised regions heterogeneity in adult vector densities is attributable to the distribution of larval breeding sites.^{3,21–23} The objective of our analysis, therefore, is to investigate the interplay between dispersal and the resource dynamism represented by the stochastic breeding sites. Simple rules governing habitat connections are used to simulate varying dispersal behaviours of *An. gambiae*, an aspect of mosquito ecology that is still poorly understood.²⁴ This type of model has been used extensively in epidemiological studies to determine the significance of connection structures in the spread and control of infectious disease.^{25–28} We use this methodology to investigate three distinct gaps in our knowledge of mosquito ecology. First, we examine the impact of mosquito dispersal on the resilience of a population to habitat instability and to control measures such as breeding site elimination. Second, we analyse the significance of productive heterogeneity (i.e. variability in the adult emergence rates) of breeding sites in the control of a population. Finally, we use this new approach to generate a falsifiable hypothesis on the survival of mosquito populations over dry seasons. Results are then discussed in the context of malaria control strategy.

Materials and Methods

Network construction

A set of 500 pools of water (or nodes, N) is simulated in 2-dimensional space using a random number generator to ascribe their x and y coordinates (where $0 < x$ and $y < \sqrt{N}$). These pools represent potential mosquito larvae habitats between which gravid females disperse. If distance has no bearing on the probability of a mosquito flying between oviposition sites, then node connections are random, resulting in an average dispersal distance of $\sqrt{N}/2$. Therefore, this random node connection structure can be perceived to be the upper limit of average dispersal distance. We shall assume that mosquitoes do not tend to disperse significantly further than 1 km between oviposition sites,²⁴ and as such, the area being simulated is in the order of 4 km². In the case of random mosquito dispersal, the probability, P , that an adult disperses between node i and node j is described by

$$P_{ij}=K/(N-1), i \neq j, \quad (1)$$

where K is the average number of connections per node. A bidirectional connection between nodes i and j is made if $U(0, 1) < P_{ij}$ where $U(a, b)$ is defined as a function that returns a random number sampled uniformly from the interval $[a, b]$. Hence, if the probability of a connection between nodes i and j is 10% ($P_{ij} = 0.1$), a dispersal path is only created when the random number generator produces a number between 0 and 0.1 (from a possible range of 0-1). In this way, stochasticity is introduced into the connectivity of nodes.

Many differential equation models implicitly assume that every node can contact any other node and, as such, the mean field case is well approximated by a network model where all connections exist (e.g. $K = N-1$; $P_{ij} = 1$). However, it would be more reasonable to assume that the spatial proximity of the larval habitats is used when computing the probability of connection between breeding sites. The spatial distance is incorporated into configuring the network using the following rule:

$$P_{ij} = \begin{cases} 0, & \text{if } i=j \\ \frac{K}{2\pi D^2} \exp\left(\frac{-d_{ij}^2}{2D^2}\right), & \text{if } i \neq j \end{cases} \quad (2)$$

where D adjusts the average length of a connection and is greater than or equal to 1.

$d_{ij} = \sqrt{(x_i - x_j)^2 + (y_i - y_j)^2}$ is the Cartesian distance between node i and node j . Figure 1 illustrates networks with the same number of nodes and connections, but with different connection structure (the network on the right appears to have fewer connections because they are shorter). The flexibility of the network architecture in describing connection structure has been capitalized upon in numerous disparate fields for decades (Albert and Barabasi, 200229).

Following Keeling (1999), the average number of connections per node (K) is held constant while the average length of connections between nodes (D) is varied to compare dispersal abilities.²⁶ Smaller values of D result in a greater probability of short connection lengths, simulating a reduced average dispersal distance of the adult mosquito. No qualitative variation arose from simulations of networks with 100, 300 and 500 nodes so only the results from 500-node networks are reported. We also repeated simulations with an average number of connections per node, K , equal to 5, 10 and 15. Again, no qualitative variation arose so only the results from $K = 5$ are presented. The spatial coordinates of the nodes were held constant throughout as changing them has no effect on the general properties of the network. However, the connections are recreated each daily time step. No two simulated networks are the same at the local level due to the stochastic nature of connection generation. However, the global properties of K and D in the individual realizations of the networks are the same. The model was written in C++ (Bloodshed Dev-C++ 1991).

Population dynamics

For an oviposited *An. gambiae* egg to develop into an adult is assumed to take eight days during the rainy season.³⁰ The rainy season is simulated because it is during this period that mosquito densities and malaria prevalence is highest.^{31–34} Following numerous studies, intraspecific competition within each larval habitat results in higher larval mortality with increasing density.^{6,34} The equation of Maynard Smith and Slatkin (1973) was used to describe larval

survival³⁵ because of its capacity to express multiple functional forms of density dependent survival data:³⁶

$$P = \frac{L_f}{1 + (\alpha \sum L)^\beta}. \quad (3)$$

P and L_f denote the number of pupae and final-instar larvae in a given pool of water respectively. Because pupal mortality is low, P is a good approximation of adult mosquitoes produced from one larval habitat. $\sum L$ is the total number of larvae of all ages. β and α determine the severity, or 'abruptness',³⁷ of density dependence and the density at which proportionate mortality reaches a fixed value. Initially, these parameters were adjusted so that at carrying capacity each habitat could give rise to 0.1 emerging female adult per day.

The duration of the mosquito's primary and successive gonotrophic cycles used in the simulation were nine and five days respectively, following empirical data collected during the rainy season in the deforested regions of the Western Kenyan highlands.³⁸ Daily adult mosquito mortality was maintained at 15%.³⁹ As a negligible proportion $(0.85^{(9+5+5+5+5)}) < 0.01$ of mosquitoes have more than 4 gonotrophic cycles, females are not considered to be reproductive beyond this stage. Only female adult mosquitoes were tracked during simulations. It is assumed that locating mates and mating did not incur any significant delay, and that locating a host and taking a blood meal requires one day.¹⁶

Dispersal ability and population resilience to habitat instability and destruction

During the rainy season, small pools are continually destroyed and reformed. The significance of the stability of these habitats has been demonstrated in field studies.³⁰ A more unstable environment is simulated by increasing the rate of habitat destruction. For simplicity, habitat destruction kills all the pre-adult stages within the habitat (although future adaptations could be incorporated to allow for partial mortalities). To simulate wet season dynamics, after a habitat is destroyed (either through land management or through natural processes) it is replaced the following day. This generates a dynamic landscape with a continually replenished potential for mosquito growth that more realistically simulates natural settings. We analyse the impact of varying the average adult dispersal distance on mosquito population persistence and determine the necessary rate of habitat destruction to bring about extinction. We also determine the impact of habitat stability and dispersal ability on population growth. A 60-day time period (2 month wet season) is simulated unless stated otherwise. Simulations take place over discrete, daily time steps.

The significance of between-habitat variability in mosquito productivity

Heterogeneity of larval habitat productivity is incorporated by assuming that the carrying capacity of the pools is a random variable following a Poisson distribution, with a mean equal to that of the homogenous-node networks. This distribution is selected because it plays a central role in the analyses of count data in ecology.⁴⁰ If n adults emerge at random across N pools, then the distribution of the numbers of emerging mosquitoes per pool will be approximately Poisson (with mean n/N), and as such this distribution does not require any additional parameter to describe its variability (c.f. Gaussian and Binomial distributions). For simplicity, we assume that the adult emergence rate increases with larval habitat size,⁴¹ and that the habitat's daily extinction risk is a linear function of its size. The impact that breeding site heterogeneity has on the extinction thresholds of mosquito populations with varying dispersal abilities is measured.

The survival of mosquito populations over seasonally dry periods

Field studies have shown that adult mosquito abundance drops substantially during the dry season.⁴² How *An. gambiae* mosquito populations survive through this period is largely unknown. Some empirical evidence suggests that mosquitoes surviving the dry season are of an older age structure.⁴³ It therefore follows that adult mosquitoes undergo behavioural/physiological changes at the onset of the dry season which enable them to aestivate during this period. The alternative hypothesis is that populations continue to breed in very limited habitats and thus at very low/undetectable densities. Determining which of these strategies is undertaken in natural settings has proven difficult due to the inability of current tools to accurately determine the age of adult mosquitoes.^{44,45} We determine the trend in mosquito population growth at the onset of a wet season in an attempt to identify any qualitative differences between the time series of populations initiated from small/undetectable populations that are utilizing the alternative strategies. We also analyse the robustness of these differences under different start conditions and dispersal abilities. In doing so, we hope to develop a testable hypothesis for mosquito perpetuation through the dry period that has real-life implications to vector management.

Results

Adult dispersal and population growth

There is a ten-fold difference in the average connection length associated with short-distanced dispersal (100 meters) compared to unrestricted, random dispersal (1 km). Initiating the simulations with 1% of the area randomly infested with mosquitoes, a non-linear relationship was found between the average adult dispersal distance and the rate of mosquito spread (Figure 2). Most notable are variations at the low end of the scale where it is shown to take twice as long for mosquitoes to oviposit in all pools when the adults' average dispersal is 100 m compared to 350 m (Figure 2). Significantly, little difference is seen in the rate of spread when comparing a dispersal distance of 350 m with random dispersal (1 km).

Dispersal, habitat heterogeneity and control

Short-ranged dispersal (100 m) was then compared to unrestricted dispersal (1 km), and the situation whereby each node is connected to all other nodes – a mean field approximation – to determine the role of adult movement in vector population dynamics. Two initial conditions were used for the simulations: 100% of habitats with larval densities at carrying capacity, meaning an adult female emerged every 10 days from every habitat, and 10% of habitats at carrying capacity, meaning an adult female emerged every 10 days from 50 of the 500 habitats. In later scenarios, heterogeneity in larval habitat carrying capacities was simulated by adjusting alpha and beta to allow for a Poisson distribution of emergence rates (see Methods). Field evidence suggests that larger, more stable habitats are also more productive to *An. gambiae* mosquitoes.⁴¹ Larger habitat size can have two effects on the extinction probability: the extinction probability can be decreased through reduced risk of the habitat drying up³⁰ or be increased through anthropogenic habitat management. Both scenarios were simulated whereby a particular habitat's extinction risk was increased or decreased as a function of its size relative to the average habitat size (Figure 3).

When larvae are initiated at carrying capacity in each habitat, environmental management is equally effective in reducing the abundance of mosquitoes exhibiting the three dispersal patterns (short-range dispersal, random dispersal, and mean field approximation; Figures 3B and 3D). This is true for populations with both homogenous and heterogeneous larval habitats. However, the relevance of vector dispersal becomes apparent when simulations are initiated with low mosquito abundance, e.g., when the simulated population is coming into a wet season from a dry season. Here, restrictions in adult dispersal delay the spread of the mosquitoes

through the area (as illustrated in Figure 2) resulting in a population that is more easily suppressed (Figures 3A and 3C).

The impact of dry-season survival strategies on population extinction

Two alternative strategies by which mosquitoes survive the dry season were simulated. The first assumed that the adults remain relatively dormant and non-productive until the onset of the rainy season. The second assumed that they continue to reproduce, albeit at low/ undetectable abundances. Irrespective of the initial vector density, average dispersal distance had little effect on the probability of population persistence (Figure 4). As expected, larger initial populations necessitated higher rates of daily habitat destruction to drive the mosquitoes to extinction (Figure 4). Regardless of the initial population level or dispersal behaviour, a population that continued to breed throughout the dry season was found to be substantially more resilient to habitat destruction, requiring approximately 60% of the habitats destroyed each day to be driven to extinction (Figure 4).

The alternative dry-season survival strategies have distinctive population dynamics

Given the significant influence that the alternative dry-season survival strategies (aestivation vs. continuous breeding) had on the extinction thresholds, time series of adult densities under both scenarios were simulated to elucidate any distinguishing characteristics. Simulations were initiated at the onset of the wet season either with 0.1 female adults emerging from 10% of pools (50 nodes) per day or 0.01 female adults emerging from all 500 pools per day. This was done to illustrate the impact of a patchy, rather than uniform, distribution of mosquitoes when abundances are low. Figure 5 shows the results of simulations of both survival strategies initiated with either a patchy or uniform distribution for short-ranged dispersal, random dispersal and the mean field approximation. Larval habitat connectivity has little effect on the overall dynamics of a mosquito population going into a rainy season when the population is initiated with a uniform distribution (Figures 5A and 5B). Mosquito dispersal becomes a more important factor when the adults have a patchy distribution at the end of the dry season (Figures 5C and 5D). Here, both short-ranged and random dispersal have notably reduced rates of population growth compared with the mean field approximation. The two dry-season survival strategies give rise to very similar overall population densities by the end of the simulated two-month rainy season, but the patterns of growth for the alternatives are distinctive. Growth is more delayed for a population that persists through the dry season as a result of extended adult longevity (Figure 5). The delay results from the time taken for the cohort of new adults to develop from the newly-oviposited eggs and to complete the first gonotrophic cycle. In this scenario, there is a reduction in the adult population abundance when this first cohort of adults senesce before adults of the next generation emerge (see the time period between 20 and 25 days following the onset of the wet season in Figures 5B and 5D). Conversely, a population initiated with mosquitoes at varying life stages does not experience the additional delay in its growth or a temporary reduction in its abundance (Figure 5) because its subpopulations are desynchronized at the onset of the wet season.

Discussion

The present study develops an alternative tool for modelling mosquito populations to examine the impact of habitat instability and adult dispersal behaviour on the abundance and persistence of a mosquito population. Previously, models of a static landscape have shown an increased resilience to habitat destruction associated with improved oviposition site locating efficiency.¹⁶ In our dynamic landscape generated through stochastic connections between temporary habitats, we have shown the relationship between adult movement and resource management to be less clear-cut. When the population is initiated at the full carrying capacity of larval habitats, we found little difference in the susceptibility to habitat instability/destruction

between mosquitoes that disperse 0.1 Km and 1 Km. That is, breeding site elimination is equally effective for short- and long-ranged dispersers when adult mosquito abundance is high. However, when initiated at densities way below the carrying capacity, we found mosquitoes that disperse further spread through the network faster and are resultantly more resilient to habitat instability/destruction.

To present transparent relationships between mosquito dispersal and control, we have had to make simplifying assumptions. To develop this theoretical framework further, it would be prudent to analyse the effect on the population dynamics of variable human dwelling distributions. Once humans are incorporated, this ecologically-derived model can be coupled with the epidemiology of malaria to create a novel type of vector-borne disease transmission model. We are in the process of making this more complex version.

Nevertheless, in examining the relationship between the adult mosquito dispersal and the larval habitats, we highlight the importance of dispersal at the low end of the range (dispersal lengths of 100–350 m), and demonstrate the model's insensitivity to variations in dispersal lengths of over 350 m. In accordance with some previous studies,^{31,46} simulations downplay the significance of between-habitat variability in female emergence rates, showing it to have minimal impact on a population's extinction risk.

This analysis also sheds light on the consequence of different dry-season strategies of *An. gambiae* mosquitoes on its population dynamics. We show that the mosquito's rate of spread and its susceptibility to habitat instability/destruction is largely dependent on which strategy it uses to survive throughout the dry season. A low-density, aging and non-productive population spreads slowly at the onset of the wet season and is more sensitive to habitat instability/destruction. Conversely, a population that continues to breed, albeit at a low density, spreads rapidly and is substantially more difficult to eliminate through resource management. With the resurging interest in integrated vector management tools for malaria control, it is important to determine which survival strategy *An. gambiae* undertakes so that a better assessment of resource management can be made. We hypothesize that if mosquito populations survive dry seasons by staving off senescent mortality, the population age structure will be more synchronized at the onset of the wet season and this should be detectable from accurately collected time series data of adult densities. We hope that our analysis highlights this critical aspect of mosquito ecology while providing a novel and flexible apparatus for modelling malaria vectors.

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Fig. 1. Networks of 100 nodes with random (left) or short-distanced (right) connections. Each network has an average of 5 connections per node.

Fig. 2.

The influence of dispersal behaviour on the spread of mosquitoes through a network. The average number of days required for adults to spread to all breeding sites (key) is shown for 100 simulated networks when 1% of breeding sites are initially infested.

Fig. 3.

The adult mosquito population density (relative to population carrying capacity) following 60 days of simulation. The key describes the adult mosquito dispersal behaviour. **A**, homogenous habitat productivity, initiated at 10% carrying capacity. **B**, homogenous habitat productivity, initiated at 100% carrying capacity. **C**, heterogeneous habitat productivity, initiated at 10% carrying capacity. **D**, heterogeneous habitat productivity, initiated at 100% carrying capacity. Results were indistinguishable when extinction probability was proportional or inversely proportional to habitat size (productivity), so only the latter scenario is plotted. Standard error bars from 100 simulations are shown.

Fig. 4.

The probability of persistence of a mosquito population is affected by the strategy it uses to survive through dry seasons. The initial habitat infestation is 1%, 10% and 100% for **A**, **B** and **C** respectively. The contour maps illustrate the persistence probabilities of populations that are initiated from a cohort of aestivating adult mosquitoes, while the broken lines denote the extinction threshold for perpetually breeding mosquito populations.

Fig. 5.

Time series for adult mosquito population growth at the onset of the wet season. The key describes the adult mosquito dispersal behaviour. The population is initiated at 10% carrying capacity. **A**, mosquitoes continue to reproduce throughout the dry season and spread from an initially uniform distribution. **B**, mosquitoes aestivate and spread from an initially uniform distribution. **C**, mosquitoes continue to reproduce throughout the dry season and spread from an initially patchy distribution. **D**, mosquitoes aestivate and spread from an initially patchy distribution.