

# Appendix S1. Full description of the models and the simulation method

## Description of model

<b>1</b>	<b>X-shredder model</b>	<b>1</b>
1.1	Non-spatial X-shredder model . . . . .	2
1.2	Spatial X-shredder model . . . . .	2
1.2.1	Demographic rates . . . . .	3
1.2.2	Movement . . . . .	3
1.2.3	Variation in landscape characteristics . . . . .	4
1.2.4	Simulation method . . . . .	4
<b>2</b>	<b>Classical HEG model</b>	<b>5</b>
2.1	Non-spatial model . . . . .	5
2.2	Spatial model . . . . .	6

## Introduction

Here we fully describe both the models and the methods used to obtain the results in the main text. We begin by describing the non-spatial model of the X-shredder genetic construct. We next develop the non-spatial model into the spatial model, and describe the simulation algorithm. Finally, we describe how the models are modified to study the classical HEG construct.

### 1 X-shredder model

As stated in the main text, the mosquito life-cycle is decomposed into a juvenile stage  $J$ , adult males  $M$ , and three adult female stages (unmated females  $U$ , mated females searching for hosts  $H$ , and ovipositing females  $O$ ). The nature of the X-shredder construct requires the model to keep track of the genotype of juveniles, which may be  $J_X$  (female),  $J_{Y_0}$  (wildtype male), or  $J_{Y_1}$  (HEG male), and adult males ( $M_{Y_0}$  or  $M_{Y_1}$ ). For mated females, it is necessary to keep track of the genotype of the male she mated with, which we denote by a superscript (e.g.  $H^{Y_0}$ ). This combination of mosquito types and genotype gives rise to 10 distinct mosquito classes  $\{(J_X, J_{Y_0}, J_{Y_1}), (M_{Y_0}, M_{Y_1}), U, (H^{Y_0}, H^{Y_1}), (O^{Y_0}, O^{Y_1})\}$ .

## 1.1 Non-spatial X-shredder model

Our non-spatial models are mean-field in the sense that interactions among individuals are governed by global mean densities of resources and con-specifics rather than by local variations in these quantities. As such, the spatial distribution of individuals has no bearing on the population's dynamics, which can thus be fully described by a set of ordinary differential equations,

$$\begin{aligned}
dJ_X/dt &= \kappa\nu \left( \frac{O^{Y_0}}{2} + \frac{1-e}{2} O^{Y_1} \right) - \gamma_J J_X - \mu_J J_X - \alpha J_X (J_X + J_{Y_0} + J_{Y_1}), \\
dJ_{Y_0}/dt &= \kappa\nu \left( \frac{O^{Y_0}}{2} \right) - \gamma_J J_{Y_0} - \mu_J J_{Y_0} - \alpha J_{Y_0} (J_X + J_{Y_0} + J_{Y_1}), \\
dJ_{Y_1}/dt &= \kappa\nu \left( \frac{1+e}{2} O^{Y_1} \right) - \gamma_J J_{Y_1} - \mu_J J_{Y_1} - \alpha J_{Y_1} (J_X + J_{Y_0} + J_{Y_1}), \\
\left( \begin{aligned} dM_G/dt &= \gamma_J J_G - \mu_M M_G \end{aligned} \right)_{G \in \{Y_0, Y_1\}}, \\
dU/dt &= \gamma_J J_X - \mu_U U - mU (M_{Y_0} + M_{Y_1}), \\
\left( \begin{aligned} dH^G/dt &= mU M_G + \nu O^G - \mu_H H^G - \gamma_H H^G \end{aligned} \right)_{G \in \{Y_0, Y_1\}}, \\
\left( \begin{aligned} dO^G/dt &= -\nu O^G - \mu_O O^G + \gamma_H H^G \end{aligned} \right)_{G \in \{Y_0, Y_1\}}.
\end{aligned}$$

The demographic parameters  $\{\kappa, \nu, \gamma_J, \alpha, \mu_J, \mu_U, \mu_M, \mu_H, \mu_O, m, \gamma_H\}$  and the cleavage rate  $e$  are defined in Table S1. Recall from the main text that  $0 \leq e \leq 1$  and the probability with which a randomly-chosen gamete from a HEG-bearing male carries the Y chromosome is  $\frac{e+1}{2}$ . The equilibrium densities can be found for any given set of parameters by numerically solving these equations after setting the left-hand sides to zero.

## 1.2 Spatial X-shredder model

To extend the non-spatial model into a spatial model, we re-define the population as a set of discrete individuals in a continuous plane. Stochasticity is incorporated by supposing that transition events such as mortality are random variables in any given time interval  $\Delta t$ . In the limit of  $\Delta t \rightarrow 0$ , the probability that a particular event occurs is  $r \times \Delta t$  where  $r$  is the appropriate rate parameter. This assumption ensures that the time intervals separating events are exponentially distributed, and the model is formally a Markov process. Henceforth, we use the term ‘‘rate’’ in the Markov sense: a measure of how quickly a particular transition occurs.

The demographic model is embedded in a landscape defined by its distribution of adult feeding and breeding sites. A feeding site is a point location that a mated female must visit in order to take a blood-meal, while a breeding site is a point location where

a blood-fed female may oviposit. We assume that mated females are able to move freely through the landscape in search of these resources.

### 1.2.1 Demographic rates

The mathematical model is described completely by the set of transition and mortality rates. We assume that the background mortality rates,  $\{\mu_J, \mu_U, \mu_M, \mu_H, \mu_O\}$ , and the juvenile emergence rate  $\gamma_J$ , are unaffected by spatial location and so correspond exactly to those of the non-spatial model. We account for local interaction among individuals by allowing the rate of mortality caused by competition, and the rate of mating, to vary with local conspecific densities. Interaction between individuals and their local environment is incorporated by allowing the rates of feeding and oviposition to vary with the local density of feeding and breeding sites.

1. **Competition.** Competition for resources occurs amongst juveniles which share the same breeding site. The rate of mortality caused by competition for an individual in a breeding site  $i$  is  $\alpha \times n_{J_i}(t)$ , where  $n_{J_i}(t)$  is the number of juveniles in the site at time  $t$ .
2. **Mating.** Mating can only occur between a male and unmated female that are within a distance  $s_M$  of one another. The mating rate of a particular unmated female at time  $t$  is  $mC_M(t)$ , where  $C_M(t)$  is the number of males within the radius  $s_M$  from her location. Note that while we do not consider explicit movement of unmated females, the parameter  $s_M$  determines the typical distance she might search to find a mate.
3. **Adult feeding.** Feeding can only occur if a female in search of hosts is within a distance  $s_H$  of a feeding site. The feeding rate of a particular female at time  $t$  is  $\gamma_H C_H(t)$  where  $C_H(t)$  is the number of feeding sites within a distance  $s_H$  from her location. On feeding, the individual becomes an ovipositing female carrying  $q$  eggs, where  $q$  is drawn from a Poisson distribution with mean  $\kappa$ , and her location is updated to that of the feeding site.
4. **Oviposition.** Oviposition can only occur if an ovipositing female is within a distance  $s_O$  of a breeding site. The oviposition rate of a particular ovipositing female at time  $t$  is  $\nu C_O(t)$  where  $C_O(t)$  is the number of breeding sites within a radius  $s_O$  from her location. On ovipositing, a female deposits  $p_X$  female and  $p_{Y_i}$  ( $i \in \{0, 1\}$ ) type  $i$  male eggs into one of the detectable breeding sites and her location is updated to that of the site.  $p_X$  and  $p_{Y_i}$  are drawn from Poisson distributions,  $\text{Pois}(\omega/2)$  and  $\text{Pois}(\omega/2)$  if the female is type  $O^{Y_0}$  and  $(\text{Pois}(\omega \frac{1-e}{2}), \text{Pois}(\omega \frac{1+e}{2}))$  if the female is type  $O^{Y_1}$ . If the sum  $p_X + p_{Y_i}$  exceeds her total store of eggs, then  $p_X$  and  $p_{Y_i}$  are accordingly reduced so that she deposits all her eggs, after which she reverts to hostseeker status.

### 1.2.2 Movement

Host-seeking and ovipositing females perform two types of movement, defined as searching and dispersal. Searching refers to movements made by females both at the

instance of feeding and at the instance of oviposition. Dispersal refers to further movements that do not coincide with feeding or oviposition.

Dispersal is controlled by three parameters referred to as the basic jump rate  $r$ , the strength of the reduction in movement near the object of search  $\beta$  ( $\beta \geq 1$ ), and maximum jump distance  $s_G$ . Specifically, a host-seeking female will make jumps at a rate  $r/\beta^{C_H(t)}$ , where  $C_H(t)$  is the number of feeding sites within the detection distance  $s_H$  at time  $t$  (note that  $r$  is the jump rate when no feeding sites are detectable). On making a jump, a new location is drawn at random from a disk of radius  $s_G$  that is centred on her starting location. Ovipositing females move in the same manner, except that the jump rate is influenced by proximity to breeding rather than feeding sites. If a female searching for an oviposition site is within a distance  $s_O$  from  $C_O(t)$  breeding sites, her jump rate will be  $r/\beta^{C_O(t)}$ .

### 1.2.3 Variation in landscape characteristics

Landscape structure is controlled by varying the density of feeding sites, breeding sites, and the covariance between the two types of site. The feeding sites are assumed to be static, and are distributed according to a spatial Poisson process with density  $\theta_A$ . Breeding sites are created at rate  $\sigma \times \theta_B$  per unit area and destroyed at rate  $\sigma$ .  $\theta_B$  thus defines the density of breeding sites and  $1/\sigma$  defines the typical longevity of a breeding site. On the destruction of a breeding site, the juveniles present in the site all die. Covariance between breeding and feeding sites is defined by the parameter  $\rho$ , such that  $\rho > 0$  indicates positive and  $\rho < 0$  negative covariance. The procedure for generating this covariance is as follows.

For the special case of no covariance between feeding and breeding sites ( $\rho = 0$ ), new breeding sites are placed in random locations so that the distribution of breeding sites, at any time  $t$ , follows a spatial Poisson process with density  $\theta_B$ . If the covariance is strictly positive or negative ( $\rho \neq 0$ ), the placement of new patches is biased by the local density of feeding sites. We define the density of feeding sites at a location  $x$ ,  $h(x)$ , as the number within a distance  $s_\rho$  of  $x$ . We generate a set of potential breeding sites,  $X$ , through a Poisson spatial process with density  $\theta_C$ . For each point  $x_i \in X$ , we define the suitability of  $x_i$ ,  $s(x_i)$ , by the function  $s(x_i) = (1 + \rho)^{h(x_i)}$ . Whenever a new breeding site is to be created, a location is drawn from  $X$  using the probability distribution  $(s(x_i)/\sum_{x_i \in X} s(x_i))_{x_i \in X}$  to choose the index  $i$ . This location is removed from the set  $X$  and a new location with random coordinates is added to  $X$ . In order to ensure  $X$  retains an approximately uniform Poisson spatial distribution, points in  $X$  are also created in random locations at rate  $\sigma_C \times \theta_C$ , and destroyed at rate  $\sigma_C$ .

### 1.2.4 Simulation method

The simulations correspond exactly to the mathematical model, except for the assumptions of finite space, and up to the accuracy of floating point arithmetic and random number generation. In the simulation algorithm, individuals are represented by their  $x$  and  $y$  coordinates in a toroidal two-dimensional space. The simulation iterates the following sequence of procedures:

1. The rates of all possible events are summed to a total event rate  $r_{tot}$ .

2. A time interval  $\Delta t$  is sampled from the exponential distribution with rate  $r_{tot}$ , so that  $\Delta t$  has mean  $1/r_{tot}$ , and the simulation time is incremented by  $\Delta t$ .
3. An event is chosen from the categorical distribution so that the probability that a particular event is chosen is proportional the rate of that event.
4. The chosen event is then implemented by the simulation code, and the rates are updated as necessary.

To investigate the process of HEG establishment, we utilised the simulation algorithm as follows. A simulation began with a stochastic realisation of a landscape, densely populated with wildtype individuals. The wildtype population dynamics were allowed to run for sufficient time to reach a quasi-equilibrium, whereby population density fluctuated around a carrying capacity. A number of adult males with the HEG construct were then introduced at a number of breeding sites, chosen randomly except for the stipulation that the sites must be occupied by larvae. After this introduction, the dynamics of the population were allowed to run until a specified end time.

## 2 Classical HEG model

### 2.1 Non-spatial model

The classical HEG model differs from the X-shredder model in terms of genetic architecture. In this model, individuals have genotypes  $W$ ,  $S$ , or  $Z$  corresponding to wildtype homozygous, heterozygous, or HEG homozygous, and we note that mated females are characterised by both their own genotype (subscript) and the genotype of the male they have mated with (superscript). We assume that the fecundity of HEG homozygous females is reduced by a factor  $1 - s$ , and the fecundity of heterozygous females is reduced by a factor  $1 - sh$ . The full set of equations for the non-spatial model is as follows.

$$\begin{aligned}
dJ_W/dt &= \kappa\nu \left( O_W^W + \frac{1-e}{2} O_W^S + (1-sh) \frac{1-e}{2} O_S^W + (1-sh) \left( \frac{1-e}{2} \right)^2 O_S^S \right) \\
&\quad - \gamma_J J_W - \mu_J J_W - \alpha J_W (J_W + J_S + J_Z), \\
dJ_S/dt &= \kappa\nu \left( \frac{1+e}{2} O_W^S + (1-sh) \frac{1+e}{2} O_S^W + (1-s) O_Z^W \right. \\
&\quad \left. + O_W^Z + (1-sh) \frac{(1+e)(1-e)}{2} O_S^S + (1-s) \frac{1-e}{2} O_Z^S + (1-sh) \frac{1-e}{2} O_S^Z \right) \\
&\quad - \gamma_J J_S - \mu_J J_S - \alpha J_S (J_W + J_S + J_Z), \\
dJ_Z/dt &= \kappa\nu \left( (1-s) O_Z^Z + (1-s) \frac{1+e}{2} O_Z^S + (1-sh) \frac{1+e}{2} O_S^Z + (1-sh) \left( \frac{1+e}{2} \right)^2 O_S^S \right) \\
&\quad - \gamma_J J_Z - \mu_J J_Z - \alpha J_Z (J_W + J_S + J_Z), \\
\left( \frac{dM_G}{dt} &= \frac{\gamma_J}{2} J_G - \mu_M M_G \right)_{G \in \{W, S, Z\}}, \\
\left( \frac{dU_G}{dt} &= \frac{\gamma_J}{2} J_G - \mu_U U - m U_G (M_W + M_S + M_Z) \right)_{G \in \{W, S, Z\}}, \\
\left( \frac{dH_G^{G'}}{dt} &= m U_G M_{G'} + \nu O_G^{G'} - \mu_H H_G^{G'} - \gamma_H H_G^{G'} \right)_{G, G' \in \{W, S, Z\}}, \\
\left( \frac{dO_G^{G'}}{dt} &= -\nu O_G^{G'} - \mu_O O_G^{G'} + \gamma_H H_G^{G'} \right)_{G, G' \in \{W, S, Z\}}.
\end{aligned}$$

## 2.2 Spatial model

The transition from non-spatial to spatial model for the classical HEG construct follows the same procedure to that of the X-shredder construct. In result, the spatial model of the classical HEG differs from its X-shredder counterpart in the following items.

1. Since the classical HEG models do not keep track of juvenile sex, the sex of emergent adults is drawn at random with an equal male/female probability.
2. At oviposition, the number of eggs a female deposits is Poisson distributed with a mean that depends on her genotype. Of this number, the distribution of genotypes is randomised after taking account of homing, which may occur during meiosis in either parent.