

# 1 Equations

The equations solved by `Mosquito23` are based on the following

$$\frac{\partial X(a, s, g, m)}{\partial t} = -d_a X + b_{s,g,m} \left[ \overbrace{X(a-1, s, g, m)}^{a>0} - \overbrace{X}^{a<N-1} \right] + \overbrace{\nabla \cdot (D_{s,g,m} \nabla X - \mathbf{V}_{s,g,m} X)}^{a=N-1} +$$

$$a = 0 \quad \left\{ \begin{array}{l} \left( \frac{K - \sum_{m^*} \alpha_{m,m^*} \sum_{s,g} \sum_{i < \max(N,1)} X(i, s, g, m^*)}{K} \right) \times \\ \sum_{\substack{g_M, g_F, \\ m_M, m_F}} h(m_M, m_F, m) \lambda(g_F, m_F) i(g_M, g_F, g) \frac{w(m_M, m_F) X(N-1, M, g_M, m_M)}{\sum_{g^*, m^*} w(m^*, m_F) X(N-1, M, g^*, m^*)} \times \\ p(g_M, g_F, m_M, m_F, s) X(N-1, F, g_F, m_F) \end{array} \right.$$

where  $a$  = age ( $0$  = newborn,  $N-1$  = adult,  $[1, N-2]$  = intermediate stages),

$s$  = sex ( $M$  or  $F$ ),

$g$  = genotype ( $w$  wildtype,  $Gw$  heterozygous GM or  $GG$  homozygous GM),

$m$  = mosquito species ( $C = An. coluzzii$ ,  $G = An. gambiae$ )

and  $X(a, s, g, m)$  is abbreviated to  $X$ .

## 2 Parameters

Parameter name	Explanation	Degrees of freedom																
$d_a$	Death rate $\begin{cases} d_{\text{adult}} & \text{for } a = N - 1 \\ d_{\text{larvae}} & \text{for } a < N - 1 \end{cases}$	2																
$b$	Larval emergence rate has distribution $\Gamma(k = N, \theta = b/N)$	1																
$D$	Diffusion rate	1																
$\mathbf{V}$	Advection vector field	Distribution of flight times																
$K$	Carrying capacity for species (spatially explicit, dependent on rainfall)	1 (for now)																
$h(m_M, m_F, m)$	Hybridisation rate (following Beeton et al. 2019) $= \begin{cases} 1 & \text{if } m = m_M = m_F \\ 0 & \text{otherwise} \end{cases}$	0  (may be set in code)																
$\lambda$	Larvae per female	1																
$i(g_M, g_F, g)$	Inheritance of genotype where $g = \{ww, Gw, GG\}$ <table><tr><td></td><td><math>ww</math></td><td><math>Gw</math></td><td><math>GG</math></td></tr><tr><td><math>ww</math></td><td><math>\{1, 0, 0\}</math></td><td><math>\{\frac{1}{2}, \frac{1}{2}, 0\}</math></td><td><math>\{0, 1, 0\}</math></td></tr><tr><td><math>Gw</math></td><td><math>\{\frac{1}{2}, \frac{1}{2}, 0\}</math></td><td><math>\{\frac{1}{4}, \frac{1}{2}, \frac{1}{4}\}</math></td><td><math>\{0, \frac{1}{2}, \frac{1}{2}\}</math></td></tr><tr><td><math>GG</math></td><td><math>\{0, 1, 0\}</math></td><td><math>\{0, \frac{1}{2}, \frac{1}{2}\}</math></td><td><math>\{0, 0, 1\}</math></td></tr></table>		$ww$	$Gw$	$GG$	$ww$	$\{1, 0, 0\}$	$\{\frac{1}{2}, \frac{1}{2}, 0\}$	$\{0, 1, 0\}$	$Gw$	$\{\frac{1}{2}, \frac{1}{2}, 0\}$	$\{\frac{1}{4}, \frac{1}{2}, \frac{1}{4}\}$	$\{0, \frac{1}{2}, \frac{1}{2}\}$	$GG$	$\{0, 1, 0\}$	$\{0, \frac{1}{2}, \frac{1}{2}\}$	$\{0, 0, 1\}$	0
	$ww$	$Gw$	$GG$															
$ww$	$\{1, 0, 0\}$	$\{\frac{1}{2}, \frac{1}{2}, 0\}$	$\{0, 1, 0\}$															
$Gw$	$\{\frac{1}{2}, \frac{1}{2}, 0\}$	$\{\frac{1}{4}, \frac{1}{2}, \frac{1}{4}\}$	$\{0, \frac{1}{2}, \frac{1}{2}\}$															
$GG$	$\{0, 1, 0\}$	$\{0, \frac{1}{2}, \frac{1}{2}\}$	$\{0, 0, 1\}$															
$p(g_M, g_F, s)$	Proportion of offspring of given sex given genotypes of parents $= \begin{cases} p(Gw, g_F, F) & = \frac{1}{2} \left( \frac{1}{a} - 1 \right) \\ p(GG, g_F, F) & = \frac{1}{2} \left( \frac{1}{a} - 1 \right) \\ 0.5 & \text{elsewhere} \end{cases}$	1 (accuracy $a$ )																
$w(m_M, m_F)$	Relative probability of female of species $m_F$ mating with male of species $m_M$ $= \begin{cases} w(C, C) = w(G, G) = 1 \\ w(C, G) = w(G, C) = w \end{cases}$	1 ( $w$ ) (defaults to $w = 0$ )																
$\alpha(m, m')$	Lotka-Volterra competition between species	Defaults to $\alpha = I$ (may be set in code)																

## 3 Mosquito23

`Mosquito23` simplifies the above equations, by assuming that the diffusion and advection is handled by other parts of the code, so that the above equations reduce to a system of ODEs. To interface with `Mosquito23`, you need to know the ordering of its vector  $X$ . For species  $m$ , genotype  $g$ , sex  $s$  and age  $a$ , this is

$$X(m + gN_{\text{species}} + sN_{\text{species}}N_{\text{genotypes}} + aN_{\text{species}}N_{\text{genotypes}}N_{\text{sexes}}), \quad (1)$$

where

- $N_{\text{species}}$  is the number of species,
- $N_{\text{genotypes}} = 3$  is the number of genotypes (with ordering  $ww = 0$ ,  $Gw = 1$ , and  $GG = 1$ )
- $N_{\text{sexes}} = 2$  is the number of sexes (with order male = 0 and female = 1)
- $N_{\text{ages}}$  (denoted by  $N$  in the above sections) is the number of ages (with ordering newborn = 0 and adult =  $N_{\text{ages}} - 1$ , with intermediate stages in between these).

The next sections write the equations explicitly and add some explanation.

### 3.1 Adults

All adult populations are governed by

$$\frac{dX(N-1, s, g, m)}{dt} = -d_{\text{adult}}X(N-1, s, g, m) + bX(N-2, s, g, m) . \quad (2)$$

Here  $N-1$  indicates the adult age bracket, and the  $N-2$  is the eldest juvenile age bracket. The first term on the right-hand side describes the mortality of adults, while the second term describes aging from the eldest juveniles. If  $N = 1$  there are no adults, and all populations are governed by the “Newborn larvae” equations, below.

### 3.2 Intermediate juveniles

For  $0 < a < N-1$ , the populations are governed by

$$\frac{dX(a, s, g, m)}{dt} = -d_{\text{larvae}}X(a, s, g, m) + b(X(a-1, s, g, m) - X(a, s, g, m)) . \quad (3)$$

For  $N \leq 2$  there are no such intermediate juveniles. The first term on the right-hand side describes the mortality of this age-bracket of juveniles, while the term involving  $b$  describes aging to/from older/younger age brackets

### 3.3 Newborn larvae

For  $a = 0$ , the populations are governed by

$$\frac{dX(0, s, g, m)}{dt} = -d_{\text{larvae}}X(0, s, g, m) - bX(a, s, g, m) + B(s, g, m) . \quad (4)$$

The first term describes mortality of newborns, while the second describes aging into the next age-bracket of juveniles. The final term describes the birth of newborn larvae. It is

$$B(s, g, m) = L\left(1 - \frac{C(m)}{K}\right) \sum_{g_M, g_F, m_M, m_F} P_{\text{offspring}}(s, g, m | g_M, g_F, m_M, m_F) P_{\text{mating}}(g_M, m_M, m_F) \lambda X(N-1, F, g_F, m_F) \quad (5)$$

This equation deserves explanations.

- $C(m)$  is the competition that a newborn feels from the rest of the larval populations. It is

$$C(m) = \sum_{a=0}^{N-2} \sum_{s=0}^{N_{\text{sexes}}-1} \sum_{g=0}^{N_{\text{genotypes}}-1} \sum_{m'=0}^{N_{\text{species}}-1} \alpha_{m, m'} X(a, s, g, m') . \quad (6)$$

Notice that this does not include adults  $a = N-1$ . If  $N = 1$ , it is assumed that the carrying-capacity still applies, and the sum over  $a$  runs from 0 to 0. The Lotka-Volterra matrix  $\alpha$  accounts for inter-specific competition. It defaults to  $\alpha = I$ , that is, newborns only feel competition from their own species.

- The function  $L(x) = 0$  if  $x \leq 0$ , while  $L(x) = x$  for  $x > 0$ . This is to ensure that if  $C(m) > K$  no newborns are produced.
- $X(N-1, F, g_F, m_F)$  is the number of adult ( $a = N-1$ ), females of genotype  $g_F$  and species  $m_F$ . So  $\lambda X(N-1, F, g_F, m_F)$  is the number of newborns produced by these female per timestep.

- $P_{\text{mating}}(g_M, m_M, m_F)$  is the probability that a male adult of genotype  $g_M$  and species  $m_M$  successfully mates with a female adult of species  $m_F$  to produce newborn. It is

$$P_{\text{mating}}(g_M, m_M, m_F) = \frac{w(m_M, m_F)X(N-1, M, g_M, m_M)}{\sum_{g'=0}^{N_{\text{genotypes}}} \sum_{m'=0}^{N_{\text{species}}} w(m', m_F)X(N-1, M, g', m')} . \quad (7)$$

The numerator is the number of matings between male of species  $m_M$  and genotype  $g_M$  and the female, while the denominator normalises the probability. The matrix  $w$  defaults to the identity.

- $P_{\text{offspring}}(s, g, m|g_M, g_F, m_M, m_F)$  is the probability the offspring will have sex  $s$ , genotype  $g$  and species  $m$ , given the genotypes and species of its parents. This is

$$P_{\text{offspring}}(s, g, m|g_M, g_F, m_M, m_F) = h(m_M, m_F, m)i(g_M, g_F, g)p(g_M, g_F, m_M, m_F, s) . \quad (8)$$

The first term,  $h$ , determines the hybridisation between species, the second determines the inheritance of genotypes, while the final term describes any sex bias in the offspring. The hybridisation defaults to  $h = 1$  if  $m_M = m_F = m$  and zero otherwise.

- Finally, these expressions are summed over all possible parental genotypes and species using  $\sum_{g_M, g_F, m_M, m_F}$ .