

Mosquito26 is heavily based on **Mosquito23**. In fact, in the computer code the “26” class is derived from the “23” code with only a small number of changes. Therefore, this documentation can be read in tandem with the **Mosquito23** documentation.

- The “2” stands for “2 sexes”: male and female.
- The “6” stands for “6 genotypes”. There are 3 alleles: wild-type, a genetic construct, and a resistant allele. This gives 6 genotypes: ww, wc, wr, cc, cr, rr.

Mosquito26 handles just the mosquito lifecycle, and assumes that diffusion and advection is handled by other parts of the code. To interface with **Mosquito23**, you need to know the ordering of its vector X , which describes the number of mosquitoes of given species, genotype, sex and age within an area (unit cell) of the model. 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_{species} is the number of species;
- $N_{\text{genotypes}} = 6$ is the number of genotypes, with ordering $ww = 0$, $wc = 1$, $wr = 2$, $cc = 3$, $cr = 4$, $rr = 5$;
- $N_{\text{sexes}} = 2$ is the number of sexes, with ordering male= 0 and female= 1;
- N_{ages} is the number of ages, with ordering newborn= 0 and adult= $N_{\text{ages}} - 1$, with intermediate stages in between these.

1 Adults

All adult populations are goverend by

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

Here $N_{\text{ages}} - 1$ indicates the adult age bracket, and the $N_{\text{ages}} - 2$ 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 $N_{\text{ages}} = 1$ then age structure is not modelled, and all populations are governed by the “Newborn larvae” equations, below.

2 Intermediate juveniles

For $0 < a < N_{\text{ages}} - 1$, the populations are governed by

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

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. For $N_{\text{ages}} \leq 2$ there are no such intermediate juveniles.

3 Newborn larvae

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

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

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

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

This expressions in this equation are:

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

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

Notice that this does not include adults $a = N_{\text{ages}} - 1$, but only newborns and juveniles. The Lotka-Volterra matrix α accounts for inter-specific competition. It defaults to $a = I$, that is, newborns only feel competition from their own species.

- $K(m)$ is the carrying capacity, which may be spatially and temporally varying. There is one further caveat: if $K(m) < K_{\min}$ for user-defined K_{\min} (which defaults to 10^{-6}) then $B = 0$ for all s, g . This helps with numerical stability in the case when $K(m)$ is time-dependent.
- The function $L(x) = 0$ if $x \leq 0$, while $L(x) = x$ for $x > 0$. This is to ensure that if $C(m) > K(m)$ no newborns of species m are produced.
- $X(N_{\text{ages}} - 1, F, g_F, m_F)$ is the number of adult ($a = N_{\text{ages}} - 1$) females of genotype g_F and species m_F .
- λ is the baseline fecundity rate, the expected number of larvae per clutch of eggs per female per day (assuming time is measured in days), assumed produced by a mating of wildtype mosquitoes. Therefore $\lambda X(N_{\text{ages}} - 1, F, g_F, m_F)$ is the number of newborns produced by these female per day.
- $P_{\text{offspring}}(s, g, m | g_M, g_F, m_M, m_F)$ is the probability the offspring will have sex s , genotype g and species m , given the genotypes and species of its parents. It is a product of terms

$$P_{\text{offspring}}(s, g, m | g_M, g_F, m_M, m_F) = P_{\text{mating}}(g, m | g_M, g_F, m_M, m_F) i(g, g_M, g_F) p(g_M, g_F, m_M, m_F, s) . \quad (7)$$

- $P_{\text{mating}}(g, m | g_M, g_F, m_M, m_F)$ is the probability that a male of genotype g_M and species m_M successfully mates with a female of genotype g_F and species m_F to produce an offspring of genotype g and species m . In `mosquito26` it does not depend on g_F , and is

$$P_{\text{mating}}(g, m | g_M, g_F, m_M, m_F) = h(m, m_M, m_F) \frac{d(m_M, m_F) j(g_M) X_{N_{\text{ages}}-1, M, g_M, m_M}}{\sum_{g'=0}^{N_{\text{genotypes}}} \sum_{m'=0}^{N_{\text{species}}} d(m', m_F) j(g') X_{N_{\text{ages}}-1, M, g', m'}} \quad (8)$$

Here:

- $h(m, m_M, m_F)$ is the proportion of offspring mosquito type m born of a mating of male type m_M and female m_F . This is $h = 1$ if $m_M = m_F = m$ (both parents and offspring are same species); while $h = 0.5$ if $m = m_M \neq m_F$ (parents are different, and offspring is same as male parent); and $h = 0.5$ if $m = m_F \neq m_M$ (parents are different, and offspring is same as female parent); and $h = 0$ in all other cases.
- $d(m_M, m_F)$ is the relative probability of mating, based on species: $d(m_M, m_F) = 1$ if $m_M = m_F$; and $d(m_M, m_F) = w$ otherwise, where w is a user-defined parameter that is typically small.
- $j(g_M)$ is the relative probability of mating based on genotype of the male parent:

$$j(g_M) = \begin{cases} 1 & \text{if } g_M \in \{ww, wr, rr\} \\ (1 - h_e s_e)(1 - h_n s_n) & \text{if } g_M \in \{wc, cr\} \\ (1 - s_e)(1 - s_n) & \text{if } g_M \in \{cc\} \end{cases} \quad (9)$$

Here h_e, s_e, h_n and s_n are user-defined parameters.

- The denominator normalises the result

- $i(g, g_M, g_F)$ describes the probability of an offspring inheriting genotype g given parents of genotypes g_M and g_F , which is defined fully below. TODO
- $p(g_M, g_F, m_M, m_F, s)$ describes sex bias of the offspring. The default is that male and female offspring are equally likely: $p = 0.5$.

4 Time integration

The ODEs in `Mosquito23` may be integrated in time using one of the following methods.

1. Explicit-Euler, where $X(t + \Delta t) = \Delta t f(X(t))$. This is fast, but results in the greatest error.

2. Runge-Kutta4, where $X(t + \Delta t)$ is given by the fourth-order Runge-Kutta formula. This is approximately 4 times slower than explicit-Euler.
3. Scipy's `solve_ivp` method. This is over 100 times slower than explicit-Euler, but is the most accurate.

In addition, adaptive time-stepping is the default. Here, the user defines Δt , and if the algorithm detects that any $X(t + \Delta t) < 0$, the time-step is solved using a number of smaller sub-time-steps, chosen to guarantee that all X remain non-negative. This type of behaviour occurs when the time-dependent carrying capacity suddenly reduces, and the explicit-Euler or Runge-Kutta4 methods produce large negative changes in population numbers, which, if allowed, would result in $X < 0$. Solving the problem using smaller sub-time-steps overcomes this problem. In this algorithm, there is a minimum Δt allowed, which defaults to 10^{-12} , below which the algorithm exits with an error.

Finally, a user-defined cutoff, c , is placed on $X(t + \Delta t)$. If $X(t + \Delta t) < c$ (at the end of a time step) then $X(t + \Delta t)$ is set to zero. This prevents anomalous round-off and precision errors from accumulating. The default value of c is 10^{-6} .