

On line material

Supplementary data. A metapopulation model to simulate West Nile virus circulation in the old world.

Model description

The model is a deterministic discrete time meta-population model with a daily time step. A population is defined here as a group of animals (vectors or hosts) that share the same location (or places for migratory populations) and that have the same annual life cycle. The epidemiological system is represented by a set Y of host populations that share during their annual life cycle a set X of locations where vector populations live. Some of the host populations are migratory and move between locations during the year.

1. State variables

A host population is described by the distribution of animals according to their health state (the set of which is denoted Z) and to their age class (the set of which is denoted W). Three health states are considered: S (susceptible), I (viraemic), and R (immune). Several age classes are also distinguished:

- n nestlings age classes numbered 1- n (N_1 : newly hatched animals, N_n : n -days old nestlings that will leave the nest the following day),
- juveniles (J) that have left the nest but do not participate in reproduction,
- reproductive adults (A).

At day t , the proportion of birds in age class a , health state z of population y is denoted $H_{y,a,z}(t)$. Regarding to species that reproduce all over the year, population size was assumed constant and, whatever the day t , $\sum_{a \in W, z \in Z} H_{y,a,z}(t) = 1$. For species with a seasonal reproduction,

population size varies during the annual life cycle, between a minimal value at the beginning

of the hatch period and a maximal value at the end of this period. Population dynamic parameters were adjusted so that the preceding equality holds on the 1st day of the hatch period.

A vector population is described by the distribution of adults according to their health state: S (susceptible), E (latent, during the extrinsic incubation period) and I (infectious: when biting, the vector will transmit the virus to the host). At day t , the proportion of vectors living at location x that have the health state z is denoted $V_{x,z}(t)$: whatever the day t , $\sum_{z \in Z} V_{x,z}(t) = 1$.

Vector abundance varies according to a site-specific parameter: $\omega_x(\tau)$, that represents the size of the population at calendar day τ (1-365), relatively to the maximal vector abundance at location x during the annual cycle: whatever the calendar day, $\omega_x(\tau) \leq 1$.

2. Population dynamic

2.1. Birds

Let $h_{x,a,z}$ denote the state of the bird population y after ageing, death and renewal processes. It is computed using Equations (1–3):

$$h_{y,A,z} = [H_{y,A,z}(t) + r_y(\tau)H_{y,J,z}(t)](1 - \mu_A) \quad (1)$$

where: τ is the calendar day,

μ_A is the daily adult mortality rate,

$r_y(\tau)$ is the daily juvenile recruitment rate in the adult age class (transfer from the J to the A age class) for host population y and calendar day τ .

$$h_{y,J,z} = [(1 - r_y(\tau))H_{y,J,z}(t) + H_{y,N_n,z}(t)](1 - \mu_J) \quad (2)$$

where μ_J is the daily juvenile mortality rate.

$$h_{y,N_i,z} = H_{y,N_{i-1},z}(t)(1 - \mu_N) \quad \text{where } \mu_N \text{ is the daily nestlings mortality rate.} \quad (3)$$

Nestling always hatch in the S state, as indicated by Eqs. 4 and 5, where $b_y(\tau)$ is the daily per-capita hatch rate for host population y and calendar day τ .

$$h_{y,N_1,S} = \sum_{z \in Z} (1 - \mu_y) b_y(\tau) H_{y,A,z}(t) \quad (4)$$

$$h_{y,N_1,I} = h_{y,N_1,R} = 0. \quad (5)$$

2.2. Vectors

Let $v_{x,z}$ denote the state of the vector population at location x after adults daily mortality and emergence. Neglecting vertical transmission of WNV, $v_{x,z}$ is computed using Equations (6–8):

$$v_{x,S} = V_{x,S}(t)(1 - \mu_v) + \mu_v \text{ where } \mu_v \text{ is the vector daily mortality rate} \quad (6)$$

$$v_{x,E} = V_{x,E}(t)(1 - \mu_v) \quad (7)$$

$$v_{x,I} = V_{x,I}(t)(1 - \mu_v). \quad (8)$$

3. Infection dynamic

3.1. Birds

At each time step, infectious vectors bite susceptible birds that become infected (Eq. 9) according to a population- and age-specific force of infection $\lambda_{y,a}(t)$. Transition rate from health state I to R is constant (Eqs. 10–12). Birds are assumed to acquire a lifelong immunity [26], there is thus no transition from R to S.

$$H_{y,a,S}(t+1) = h_{y,a,S}(1 - \lambda_{y,a}(t)) \quad (9)$$

$$H_{y,a,I}(t+1) = h_{y,a,I}(1 - 1/T_v) + h_{y,a,S} \lambda_{y,a}(t) \quad (10)$$

where T_v is the duration of viraemia (health state I) in days.

$$H_{y,a,R}(t+1) = h_{y,a,R} + h_{y,a,I}(1/T_v) \quad (11)$$

The force of infection is computed according to Equation (12):

$$\lambda_{y,a}(t) = 1 - \exp(-RR_a K_x \omega_x(\tau) v_{x,I} (1/Tg_x)) \quad (12)$$

where: – x is the location of population y at time step t ,

– K_x is the vector-host ratio for location x , when vector abundance reaches its maximal value, *i.e.* $\omega_x(\tau) = 1$,

– RR_a is the bite relative risk for age class a ,

– Tg_x is the duration of the gonotrophic cycle for vectors living at location x (days).

In Equation (12) the number of infectious bites per host is assumed to follow a Poisson distribution. The expression $1/Tg_x$ denotes the proportion of vectors that bite a host at a given day, and $v_{x,I}$ is the proportion of infectious vectors. Thus, taking into account age-specific bite relative risk as well as the yearly variations of vector abundance, the expression $RR_a K_x \omega_x(\tau) v_{x,I} (1/Tg_x)$ denotes the number of infectious bites per host of age class a . Considering this number as the parameter of the Poisson distribution, Equation 12 gives the probability that, for a given bird of population y and age class a , the number of infectious bites is not zero.

3.2. Vectors

At each time step, susceptible vectors bite viraemic birds and become infected (Eq. 14) according to a site-specific force of infection $\lambda_x(t)$. Transition rate from health state E to I is constant (Eqs. 13–15).

$$V_{x,S}(t+1) = v_{x,S} (1 - \lambda_x(t)) \quad (13)$$

$$V_{x,E}(t+1) = v_{x,E} (1 - 1/T_x) + v_{x,S} \lambda_x(t) \quad (14)$$

where Tx_x is the duration of the extrinsic incubation period of vectors living at location x (state E).

$$V_{x,I}(t+1) = v_{x,I} + v_{x,E}(1/Tx_x). \quad (15)$$

The force of infection applied to vectors living at location x is defined in Equation (16):

$$\lambda_x(t) = \frac{1}{Tg_x} \sum_{y \in Y} \sum_{a \in W} q_{y,a} p_{y,a} \quad (16)$$

where: – $q_{y,a}$ is the proportion of bites that occur on birds of population y and age

class a :

$$q_{y,a} = \frac{\omega_{x,y}(t) RR_a \sum_{z \in Z} h_{y,a,z}}{\sum_{y' \in Y} \sum_{a \in W} \sum_{z \in Z} \omega_{x,y'}(\tau) RR_a h_{y',a,z}}$$

with $\omega_{x,y}(\tau)$ the demographic importance of population y at location x at the calendar day τ (zero if the population is not present);

– $p_{y,a}$ is the proportion of viraemic birds in population y and age class a :

$$p_{y,a} = \frac{h_{y,a,I}}{\sum_{z \in Z} h_{y,a,z}}.$$

In Equation (16), the force of infection is the product of the proportion of vectors that bite $1/Tg_x$ by the proportion of bites that occur on a viraemic bird. To compute the latter term, because of age-specific bite relative risk and because several populations may be present, we sum the prevalence rates of viraemic birds $p_{y,a}$ in the different populations and age classes, and weight each prevalence by the proportion of bites that occur on the corresponding birds $q_{y,a}$.

3.3. Incidental hosts

The daily infection rate of incidental hosts is assumed proportional to that of adult birds living

at the same place, the proportionality factor being host-specific. The incidence rate of infections in incidental hosts over a given time period from day t_1 to day t_2 may then be computed using Equation (17):

$$p_{x,h} = 1 - \exp\left(-\varphi_h \sum_{t=t_1}^{t_2} \lambda_{y,A}(t)\right) \quad (17)$$

where: – y is the resident bird population living at location x ,

– φ_h is the bite relative risk for host h , taking as a reference the force of infection for adult birds.