

# ENVIRONMENTAL NOISE AND ROSS-MACDONALD TRANSMISSION: NOTES

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## 1. BASE MODEL

Our base model is a simple version of the Ross-Macdonald model. Let  $H$  denote the number of infectious human hosts and  $V$  the number of infectious mosquitoes. The transmission of the mosquito-borne pathogen is described by the following system of equations:

$$(1.1) \quad \begin{aligned} \frac{dH}{dt} &= \frac{b\tau_{HV}}{N_H} V (N_H - H) - \gamma_H H, \\ \frac{dV}{dt} &= \frac{b\tau_{VH}}{N_H} H (N_V - V) - \mu_V V, \end{aligned}$$

where  $N_H = H + S_H$  and  $N_V = V + S_V$ . The basic reproduction number of this model is given by  $\mathcal{R}_0 = \sqrt{\frac{b^2\tau_{HV}\tau_{VH}N_V}{\mu_V\gamma_HN_H}}$  and the unique endemic equilibrium by

$$(1.2) \quad \begin{aligned} H^* &= N_H \left( \frac{\frac{b\tau_{HV}N_V}{\gamma_HN_H}}{\frac{b\tau_{HV}N_V}{\gamma_HN_H} + 1} \right) \left( \frac{\mathcal{R}_0^2 - 1}{\mathcal{R}_0^2} \right) \\ V^* &= N_V \left( \frac{\frac{b\tau_{VH}}{\mu_V}}{\frac{b\tau_{VH}}{\mu_V} + 1} \right) \left( \frac{\mathcal{R}_0^2 - 1}{\mathcal{R}_0^2} \right) \end{aligned}$$

## 2. STOCHASTIC VERSION OF THE MODEL

Here we follow the methods in O'Regan et al., 2016 which are derived from the Allen, 2010 textbook. (This will be almost word-for-word from the Appendix A of O'Regan et al., 2016, so do not use for publication purposes.)

**2.1. Demographic stochasticity.** To begin we write down a discrete stochastic process version of the model, listing each event that can occur and its corresponding transition probability. Let  $X(t) = (H(t), V(t))^T$ . To apply the diffusion approximation, we calculate the expectation vector and the covariance matrix for the change in state vector,  $\Delta X = (\Delta H, \Delta V)^T$  where  $\Delta H = H(t+1) - H(t)$ .

We first build a table of transitions.

$i$	Process	Change, $(\Delta X)_i$	Probability, $p_i$
1	New host infection	$(1, 0)^T$	$\frac{b\tau_{HV}}{N_H} V (N_H - H) \Delta t$
2	Host recovery	$(-1, 0)^T$	$\gamma_H H \Delta t$
3	New vector infection	$(0, 1)^T$	$\frac{b\tau_{VH}}{N_H} H (N_V - V) \Delta t$
4	Vector recovery	$(0, -1)^T$	$\mu_V V \Delta t$
5	No change	$(0, 0)^T$	$\left[ 1 - \sum_{i=1}^4 p_i \right] \Delta t$

From this table, we can derive the expectation as  $E(\Delta X) = \sum_{i=1}^5 p_i(\Delta X)_i$

$$\begin{aligned}
E(\Delta X) &= \sum_{i=1}^5 p_i(\Delta X)_i \\
&= p_1(\Delta X)_1 + p_2(\Delta X)_2 + p_3(\Delta X)_3 + p_4(\Delta X)_4 + p_5(\Delta X)_5 \\
&= p_1 \begin{pmatrix} 1 \\ 0 \end{pmatrix} + p_2 \begin{pmatrix} -1 \\ 0 \end{pmatrix} + p_3 \begin{pmatrix} 0 \\ 1 \end{pmatrix} + p_4 \begin{pmatrix} 0 \\ -1 \end{pmatrix} + p_5 \begin{pmatrix} 0 \\ 0 \end{pmatrix} \\
&= \begin{pmatrix} \frac{b\tau_{HV}}{N_H} V (N_H - H) \Delta t \\ 0 \end{pmatrix} + \begin{pmatrix} -\gamma_H H \Delta t \\ 0 \end{pmatrix} + \begin{pmatrix} 0 \\ \frac{b\tau_{VH}}{N_H} H (N_V - V) \Delta t \end{pmatrix} + \begin{pmatrix} 0 \\ -\mu_V V \Delta t \end{pmatrix} + p_5 \begin{pmatrix} 0 \\ 0 \end{pmatrix} \\
&= \begin{pmatrix} \frac{b\tau_{HV}}{N_H} V (N_H - H) - \gamma_H H \\ \frac{b\tau_{VH}}{N_H} H (N_V - V) - \mu_V V \end{pmatrix} \Delta t \\
&= \mu \Delta t
\end{aligned}$$

The covariance matrix associated with these changes is a 2 by 2 matrix given by  $\Sigma(\Delta X) = E([\Delta X][\Delta X]^T) - E(\Delta X)E(\Delta X)^T$ . The covariance matrix can be approximated to order  $\Delta t$  by  $\Sigma(\Delta X) \approx E([\Delta X][\Delta X]^T) = M(t)\Delta t$ :

$$\begin{aligned}
E([\Delta X][\Delta X]^T) &= \sum_{i=1}^5 p_i(\Delta X)_i(\Delta X)_i^T \\
&= p_1(\Delta X)_1(\Delta X)_1^T + p_2(\Delta X)_2(\Delta X)_2^T + p_3(\Delta X)_3(\Delta X)_3^T + p_4(\Delta X)_4(\Delta X)_4^T + p_5(\Delta X)_5(\Delta X)_5^T \\
&= p_1 \begin{pmatrix} 1 \\ 0 \end{pmatrix} \begin{pmatrix} 1 & 0 \end{pmatrix} + p_2 \begin{pmatrix} -1 \\ 0 \end{pmatrix} \begin{pmatrix} -1 & 0 \end{pmatrix} + p_3 \begin{pmatrix} 0 \\ 1 \end{pmatrix} \begin{pmatrix} 0 & 1 \end{pmatrix} + p_4 \begin{pmatrix} 0 \\ -1 \end{pmatrix} \begin{pmatrix} 0 & -1 \end{pmatrix} + p_5 \begin{pmatrix} 0 \\ 0 \end{pmatrix} \begin{pmatrix} 0 & 0 \end{pmatrix} \\
&= p_1 \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix} + p_2 \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix} + p_3 \begin{pmatrix} 0 & 0 \\ 0 & 1 \end{pmatrix} + p_4 \begin{pmatrix} 0 & 0 \\ 0 & 1 \end{pmatrix} \\
&= \begin{pmatrix} \frac{b\tau_{HV}}{N_H} V (N_H - H) + \gamma_H H & 0 \\ 0 & \frac{b\tau_{VH}}{N_H} H (N_V - V) + \mu_V V \end{pmatrix} \Delta t \\
&= M(t)\Delta t
\end{aligned}$$

Now let  $B(t) = \sqrt{M(t)}$ . Since  $M(t)$  is diagonal, computing its square root is straight-forward:

$$B(t) = \begin{pmatrix} \sqrt{\frac{b\tau_{HV}}{N_H} V (N_H - H) + \gamma_H H} & 0 \\ 0 & \sqrt{\frac{b\tau_{VH}}{N_H} H (N_V - V) + \mu_V V} \end{pmatrix}$$

The probability distribution of solutions to the discrete-valued continuous process satisfying the appropriate forward Kolmogorov equation is identical to the distribution of solutions to the following system of stochastic differential equations:

$$\begin{aligned}
dH &= \mu_1 dt + B_{11} dW_1, \\
dV &= \mu_2 dt + B_{22} dW_2,
\end{aligned}$$

where  $dW_i$  are independent standard Wiener processes. Plugging in all the symbols, we get:

$$\begin{aligned}
dH &= \left( \frac{b\tau_{HV}}{N_H} V (N_H - H) - \gamma_H H \right) dt + \sqrt{\frac{b\tau_{HV}}{N_H} V (N_H - H) + \gamma_H H} dW_1, \\
dV &= \left( \frac{b\tau_{VH}}{N_H} H (N_V - V) - \mu_V V \right) dt + \sqrt{\frac{b\tau_{VH}}{N_H} H (N_V - V) + \mu_V V} dW_2.
\end{aligned} \tag{2.1}$$

**2.2. Environmental stochasticity.** To add environmental variation, we add environmental perturbation to system 2.1 which scales with the parameter/rate that we are assuming is altered by the environment. We assume that the stochastic process obtained from the diffusion approximation is perturbed by an additional environmental noise term that scales with the mean level of the rate impacted by the environment at time

$t$ . Specifically, in a small time interval  $\Delta t$ , we assume each relevant parameter  $g$  is subject to environmental stochasticity as follow

$$g(t) \Delta t = g_0 \Delta t + \sigma \eta \sqrt{\Delta t}$$

where  $\eta$  is a normal random variable with mean zero and unit variance and  $\sigma$  denotes the strength of the environmental noise.

We modify system 2.1 as follows:

$$\begin{aligned} dH &= \mu_1 dt + G_{11} dW_1 + G_{13} dW_3, \\ dV &= \mu_2 dt + G_{22} dW_2 + G_{23} dW_3, \end{aligned}$$

where  $G = \begin{pmatrix} B_{11} & 0 & G_{13} \\ 0 & B_{22} & G_{23} \end{pmatrix}$ .

If we just focus on the effect of environmental variability on mosquito traits, we only need to look at the following parameters:  $b, \tau_{VH}$ , and  $\mu_V$ . For these parameters, we get the following matrices for  $G$ :

$$\begin{aligned} G_b &= \begin{pmatrix} B_{11} & 0 & \sigma \frac{\tau_{HV}}{N_H} V (N_H - H) \\ 0 & B_{22} & \sigma \frac{\tau_{VH}}{N_H} H (N_V - V) \end{pmatrix} \\ G_{\tau_{VH}} &= \begin{pmatrix} B_{11} & 0 & 0 \\ 0 & B_{22} & \sigma \frac{b}{N_H} H (N_V - V) \end{pmatrix} \\ G_{\mu_V} &= \begin{pmatrix} B_{11} & 0 & 0 \\ 0 & B_{22} & \sigma V \end{pmatrix} \end{aligned}$$

The level of environmental noise is controlled by  $\sigma$ . For convenience, I'll write out the full models for each of these cases below.

#### 2.2.1. Environmental variation affects biting rate, $b$ .

$$\begin{aligned} dH &= \left( \frac{b\tau_{HV}}{N_H} V (N_H - H) - \gamma_H H \right) dt + \sqrt{\frac{b\tau_{HV}}{N_H} V (N_H - H) + \gamma_H H} dW_1 + \sigma \frac{\tau_{HV}}{N_H} V (N_H - H) dW_3, \\ dV &= \left( \frac{b\tau_{VH}}{N_H} H (N_V - V) - \mu_V V \right) dt + \sqrt{\frac{b\tau_{VH}}{N_H} H (N_V - V) + \mu_V V} dW_2 + \sigma \frac{\tau_{VH}}{N_H} H (N_V - V) dW_3. \end{aligned}$$

#### 2.2.2. Environmental variation affects mosquito competence, $\tau_{VH}$ .

$$\begin{aligned} dH &= \left( \frac{b\tau_{HV}}{N_H} V (N_H - H) - \gamma_H H \right) dt + \sqrt{\frac{b\tau_{HV}}{N_H} V (N_H - H) + \gamma_H H} dW_1, \\ dV &= \left( \frac{b\tau_{VH}}{N_H} H (N_V - V) - \mu_V V \right) dt + \sqrt{\frac{b\tau_{VH}}{N_H} H (N_V - V) + \mu_V V} dW_2 + \sigma \frac{b}{N_H} H (N_V - V) dW_3. \end{aligned}$$

#### 2.2.3. Environmental variation affects mosquito mortality, $\mu_V$ .

$$\begin{aligned} dH &= \left( \frac{b\tau_{HV}}{N_H} V (N_H - H) - \gamma_H H \right) dt + \sqrt{\frac{b\tau_{HV}}{N_H} V (N_H - H) + \gamma_H H} dW_1, \\ dV &= \left( \frac{b\tau_{VH}}{N_H} H (N_V - V) - \mu_V V \right) dt + \sqrt{\frac{b\tau_{VH}}{N_H} H (N_V - V) + \mu_V V} dW_2 + \sigma V dW_3. \end{aligned}$$

#### 2.2.4. Environmental variation affects all relevant mosquito traits, $b, \tau_{VH}, \mu_V$ .

$$\begin{aligned} dH &= \left( \frac{b\tau_{HV}}{N_H} V (N_H - H) - \gamma_H H \right) dt + \sqrt{\frac{b\tau_{HV}}{N_H} V (N_H - H) + \gamma_H H} dW_1 + \sigma \alpha_b \frac{\tau_{HV}}{N_H} V (N_H - H) dW_3, \\ dV &= \left( \frac{b\tau_{VH}}{N_H} H (N_V - V) - \mu_V V \right) dt + \sqrt{\frac{b\tau_{VH}}{N_H} H (N_V - V) + \mu_V V} dW_2 + \dots \\ &\quad \dots + \sigma \left( \alpha_b \frac{\tau_{VH}}{N_H} H (N_V - V) + \alpha_\tau \frac{b}{N_H} H (N_V - V) + \alpha_\mu V \right) dW_3. \end{aligned}$$

where the  $\alpha_g$ 's represent the relative impact of environmental variation on mosquito trait  $g$ .