Isotopic incorporation and the temporal dynamics of foraging among individuals and within populations

Abstract.

1. Introduction

2. Time-dependent Ornstein-Uhlenbeck process

We can define the evolution of the concentration of a particular isotope in the predator tissue by the following Langevin equation,

$$\mathrm{d}X(t) = -\lambda \left(X(t) - \mu(t)\right) \mathrm{d}t + \lambda\sigma(t)\mathrm{d}W \tag{1}$$

where, X is the isotope-concentration, λ is the tissue-dependent incorporation rate, $\mu(t)$ and $\sigma(t)$ are the time-dependent average and standard-deviations of isotope-concentration over the prey.

2.1. Expectation

We can find the expectation of $X(t)$ as follows,

$$\mathrm{d}X + \lambda \left(X(t) - \mu(t)\right) \mathrm{d}t = \lambda\sigma(t)\mathrm{d}W \tag{2}$$

Multiplying throughout by the integrating factor, $e^{\lambda t}$ and integrating both sides w.r.t t, we get

$$\int_{t=0}^{t} \mathrm{d}\left(e^{\lambda t}\left(X - \mu\right)\right) + \int_{t=0}^{t} e^{\lambda t'}\frac{\mathrm{d}\mu}{\mathrm{d}t'}\mathrm{d}t' = \int_{t=0}^{t} \lambda e^{\lambda t'}\sigma(t')\mathrm{d}W' \tag{3}$$

Taking the expectation of both sides, the RHS reduces to zero as $\mathbb{E}(\mathrm{d}W) = 0$ and we get,

$$\mathbb{E}(X(t)) = X_0 e^{-\lambda t} + \lambda e^{-\lambda t}\int_{t'=0}^{t} \mu(t')e^{\lambda t'}\mathrm{d}t' \tag{4}$$

2.2. Variance

Similarly for the variance, we square Eq. (3), to get

$$\left(e^{\lambda t}X - X_0 - \lambda\int_0^t \mu e^{\lambda t'}\mathrm{d}t'\right)^2 = \lambda^2\int_0^t\int_0^t e^{\lambda(t'+t'')}\sigma(t')\sigma(t'')\mathrm{d}W(t')\mathrm{d}W(t'') \tag{5}$$

Taking the expectation on both sides, in the RHS, using the property, $\mathbb{E}(\mathrm{d}W(t')\mathrm{d}W(t'')) = \delta(t' - t'')\mathrm{d}t'\mathrm{d}t''$, we get,

$$\mathbb{E}\left(e^{\lambda t}X - X_0 - \lambda\int_0^t \mu e^{\lambda t'}\mathrm{d}t'\right)^2 = \lambda^2\int_0^t e^{2\lambda t'}(\sigma(t'))^2\mathrm{d}t' \tag{6}$$

Let us call the integrals $\int_0^t \mu(t')e^{\lambda t'}\mathrm{d}t'$ and $\int_0^t e^{2\lambda t'}(\sigma(t'))^2\mathrm{d}t'$ as $\mathcal{U}$ and $\mathcal{S}^2$ and expanding the LHS, we get

$$e^{2\lambda t}\mathbb{E}(X^2) + X_0^2 + \lambda^2\mathcal{U}^2 - 2X_0\mathbb{E}(X)e^{\lambda t} - 2X_0\lambda\mathcal{U} - 2\lambda e^{\lambda t}\mathbb{E}(X)\mathcal{U} = \lambda^2\mathcal{S}^2 \tag{7}$$

And so the variance is given by,

$$\begin{aligned}\mathbb{V}(X) &= \mathbb{E}(X^2) - (\mathbb{E}(X))^2 \\ &= \lambda^2 e^{-2\lambda t}\mathcal{S}^2 - X_0^2 e^{-2\lambda t} - \lambda^2 e^{-2\lambda t}\mathcal{U}^2 + 2X_0\mathbb{E}(X)e^{-\lambda t} + 2X_0\lambda e^{-2\lambda t}\mathcal{U} + 2\lambda e^{-\lambda t}\mathbb{E}(X)\mathcal{U} - (\mathbb{E}(X))^2\end{aligned} \tag{8}$$

$$\mathbb{V}(X) = \lambda^2 e^{-2\lambda t}\int_0^t e^{2\lambda t'}(\sigma(t'))^2 \mathrm{d}t' \tag{9}$$

where, to go from Eq. (8) to Eq. (9) we used $\mathbb{E}(X)$ given by Eq. (4).

2.3. Sinusoidal input

Suppose the inputs $\mu(t)$ and $\sigma(t)$ to the system are sinusoidal, i.e,

$$\mu(t) = a_1 + b_1 \sin(\omega t)\ , \quad \sigma(t) = a_2 + b_2 \sin(\omega t) \tag{10}$$

Using Eq. (4) and Eq. (9), we get

$$\mathbb{E}(X) = X_0 e^{-\lambda t} + a_1\left(1 - e^{-\lambda t}\right) + \frac{b_1\omega\lambda}{\lambda^2+\omega^2}e^{-\lambda t} + \frac{b_1\lambda}{\sqrt{\lambda^2+\omega^2}}\sin\left(\omega t + \tan^{-1}\left(\frac{\omega}{\lambda}\right)\right) \tag{11}$$

$$\begin{aligned}\mathbb{V}(X) = &\frac{1}{4}\lambda\left(2a_2^2+b_2^2\right)\left(1-e^{-2\lambda t}\right) + e^{-2\lambda t}\lambda^2\left(\frac{b_2^2\lambda}{4(\lambda^2+\omega^2)} + \frac{2a_2b_2\omega}{4\lambda^2+\omega^2}\right) \\ &+ \frac{2a_2b_2\lambda^2}{\sqrt{4\lambda^2+\omega^2}}\sin\left(\omega t + \tan^{-1}\left(\frac{\omega}{2\lambda}\right)\right) - \frac{b_2^2\lambda^2}{4\sqrt{\lambda^2+\omega^2}}\sin\left(2\omega t + \tan^{-1}\left(\frac{\lambda}{\omega}\right)\right)\end{aligned} \tag{12}$$

Getting rid of transients, we get,

$$\mathbb{E}(X) = a_1 + \frac{b_1\lambda}{\sqrt{\lambda^2+\omega^2}}\sin\left(\omega t + \tan^{-1}\left(\frac{\omega}{\lambda}\right)\right) \tag{13}$$

$$\begin{aligned}\mathbb{V}(X) = \frac{1}{4}\lambda\left(2a_2^2+b_2^2\right) &+ \frac{2a_2b_2\lambda^2}{\sqrt{4\lambda^2+\omega^2}}\sin\left(\omega t + \tan^{-1}\left(\frac{\omega}{2\lambda}\right)\right) \\ &- \frac{b_2^2\lambda^2}{4\sqrt{\lambda^2+\omega^2}}\sin\left(2\omega t + \tan^{-1}\left(\frac{\lambda}{\omega}\right)\right)\end{aligned} \tag{14}$$

If we time-average over the oscillations, we get,

$$\langle\mathbb{E}(X)\rangle_t = a_1\ , \quad \langle\mathbb{V}(X)\rangle_t = \frac{1}{4}\lambda\left(2a_2^2+b_2^2\right) \tag{15}$$

3. On the input to the O-U equation

In the previous section we had assumed $\mu(t)$ and $\sigma(t)$ was given by some underlying dynamics. One possible way to incorporate the dynamics is to assume a Lotka-Volterra system. The simplest system where we can expect prey switching behavior is a Lotka-Volterra system with one predator and two preys. We have,

$$\begin{aligned} \dot{c} &= -r_0 c + acn_1 + acn_2 \\ \dot{n}_1 &= r_1 n_1 - cn_1 \\ \dot{n}_2 &= r_2 n_2 - cn_2 \end{aligned} \tag{16}$$

where c is the number density of the consumer, n_i are the number densities of the prey. The dynamics we adopt are deterministic. However, we introduce noise in the encounter rates as follows. We define the encounters as a Poisson process with encounter rate given by a gamma distribution with parameters $(n_i/v, 1/v)$. Here v is the 'patchiness' or the additional variance to constant rate Poisson process. For simplicity we assume the patchiness is the same accross the preys. Imposing constant feeding rate, we combine the two independent gamma distribution to a two variable Dirichlet distribution with parameters $(n_1/v, n_2/v)$.