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,

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