STOCHASTIC POPULATION MODELS (SPRING 2015)

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2. Fluctuating parameters in a single-ODE model

2.1. **The general idea.** Consider the scalar population equation

$$\frac{dx}{dt} = f(x, \theta) \tag{1}$$

where θ is a scalar parameter. How would x respond to fluctuations in θ? We study the response to small fluctuations near a stable equilibrium. Suppose

$$\begin{aligned} f(\bar{x}, \bar{\theta}) &= 0 \\ \partial_x f(\bar{x}, \bar{\theta}) &< 0 \end{aligned} \tag{2}$$

i.e., that $x = \bar{x}$ is a stable equilibrium for given constant $\theta = \bar{\theta}$.

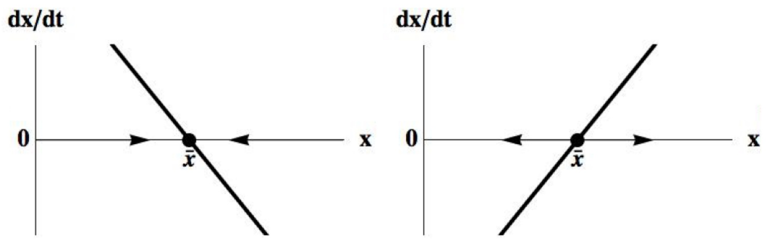

Figure 1. Stability and instability of $\bar{x}$ depending on the slope of $f(x, \bar{\theta})$.

If $\bar{x}$ is stable, then small fluctuations in θ around $\bar{\theta}$ will cause only small fluctuations in x around $\bar{x}$. We write

$$\begin{aligned} x(t) &= \bar{x} + \xi(t) \\ \theta(t) &= \bar{\theta} + \eta(t) \end{aligned} \tag{3}$$

where $\xi(t)$ and $\eta(t)$ are the deviations of, respectively, x from $\bar{x}$ and θ from $\bar{\theta}$. If $|\xi(t)|$ and $|\eta(t)|$ are uniformly small (i.e., for all $t \geq 0$), then we can replace the population equation by the linear approximation

$$\frac{d\xi}{dt} = \partial_x f(\bar{x}, \bar{\theta})\xi + \partial_\theta f(\bar{x}, \bar{\theta})\eta \tag{4}$$

The solution of the linear system is

$$\xi(t) = \xi(t_0)e^{(t-t_0)\partial_x f(\bar{x},\bar{\theta})} + \partial_\theta f(\bar{x},\bar{\theta}) \int_{t_0}^{t} \eta(\tau) e^{(t-\tau)\partial_x f(\bar{x},\bar{\theta})} d\tau \tag{5}$$

Since by assumption $\partial_x f(\bar{x},\bar{\theta}) < 0$, the first term converges to zero as $t \to \infty$ (or $t_0 \to -\infty$) and therefore is called the transient part of the solution. We are interested in the the persistent solution, i.e.,

$$\xi(t) = \partial_\theta f(\bar{x},\bar{\theta}) \int_{-\infty}^{t} \eta(\tau) e^{(t-\tau)\partial_x f(\bar{x},\bar{\theta})} d\tau \tag{6}$$

Notice that the above defines a linear map $\Lambda : \eta \longmapsto \xi$ that converts fluctuations in η into fluctuations in ξ, i.e., converts fluctuations in the "input" θ into fluctuations in the "output" x. In particular, we have

$$e^{i\omega t} \overset{\Lambda}{\longmapsto} \frac{\partial_\theta f(\bar{x},\bar{\theta})}{i\omega - \partial_x f(\bar{x},\bar{\theta})} \cdot e^{i\omega t} \tag{7}$$

i.e., $\eta(t) = e^{i\omega t}$ is an eigenfuction of Λ with corresponding eigenvalue

$$T(\omega) = \frac{\partial_\theta f(\bar{x},\bar{\theta})}{i\omega - \partial_x f(\bar{x},\bar{\theta})}, \tag{8}$$

which is called the transfer function.

The theory of Fourier series tells us that every (sufficiently smooth) periodic function can be written as a linear combination of countably many functions of the form $e^{i\omega t}$ for different values of ω. As a simple example, consider

$$\sin(\omega t) = \frac{e^{i\omega t} - e^{-i\omega t}}{2i} \tag{9}$$

Exploiting the linearity of Λ and the fact that $e^{i\omega t}$ and $e^{-i\omega t}$ are eigenfunctions with respective eigenvalues $T(\omega)$ and $T(-\omega)$, we have

$$\sin(\omega t) \overset{\Lambda}{\longmapsto} \frac{T(\omega)e^{i\omega t} - T(-\omega)e^{-i\omega t}}{2i} \tag{10}$$

which can be written more conveniently as

$$\sin(\omega t) \overset{\Lambda}{\longmapsto} |T(\omega)| \sin\big(\omega t + \arg T(\omega)\big) \tag{11}$$

where $|T(\omega)|$ is the modulus of the transfer function and $\arg T(\omega)$ its argument.

The significance of the transfer function now becomes clear: (*i*) $|T(\omega)|$ is the ω-dependent gain, i.e., the factor by which fluctuations in the input θ of the specific frequency ω are amplified in the output x; (*ii*) $\arg T(\omega)$ is the phase-shift between the output and the input for fluctuations of the specific frequency ω.

2.2. **The population as a filter.** If the input θ combines different frequencies, then some of these frequencies are suppressed in the output x while others are

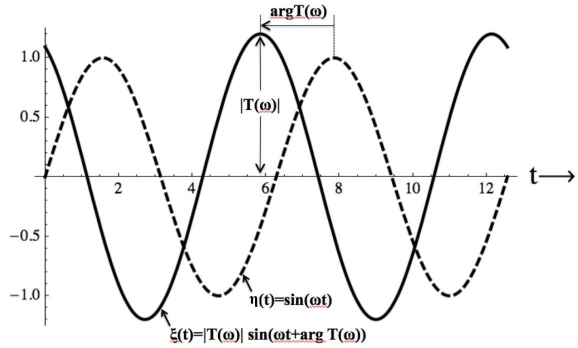

FIGURE 2. The action of $\Lambda : \eta \mapsto \xi$.

amplified, and the phase-shift in the response is different for different frequencies as well. The population thus acts as a filter on the input signal.

For small fluctuations in the input, the filter characteristics of the population are given by the modulus and the argument of the transfer function. From equation (8) we have

$$|T(\omega)| = \frac{|\partial_\theta f(\bar{x}, \bar{\theta})|}{\sqrt{\omega^2 + \partial_x f(\bar{x}, \bar{\theta})^2}} \tag{12}$$

which is a decreasing function of $|\omega|$, i.e., high frequencies are suppressed, and so the population acts as a low-pass filter.

A low-pass filter is characterized by its maximum gain (G_m) and the cutoff frequency (ω_c). The latter defines the band width of the filter. The meaning of the G_m and the ω_c becomes clear if we plot $|T(\omega)|$ against $|\omega|$ on a double logarithmic scale.

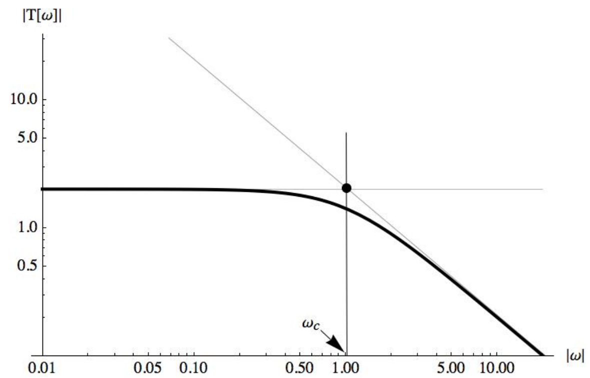

FIGURE 3. The gain as a function of signal frequency.

From equation (12) we get for small values of $|\omega|$

$$\log T(\omega) \approx \log \frac{|\partial_\theta f(\bar{x}, \bar{\theta})|}{|\partial_x f(\bar{x}, \bar{\theta})|} =: \log G_{\mathrm{m}} \tag{13}$$

Moreover, for large values of $|\omega|$ we get

$$\log |T(\omega)| \approx \log |\partial_\theta f(\bar{x}, \bar{\theta})| - \log |\omega| \tag{14}$$

The intersection of the two approximations gives us an explicit expression for the cutoff frequency

$$\omega_{\mathrm{c}} = |\partial_x f(\bar{x}, \bar{\theta})| \tag{15}$$

From equation (8) we have

$$\arg T(\omega) = \arctan\left(\frac{\omega}{\partial_x f(\bar{x}, \bar{\theta})}\right) \tag{16}$$

for the frequency-dependent phase shift.

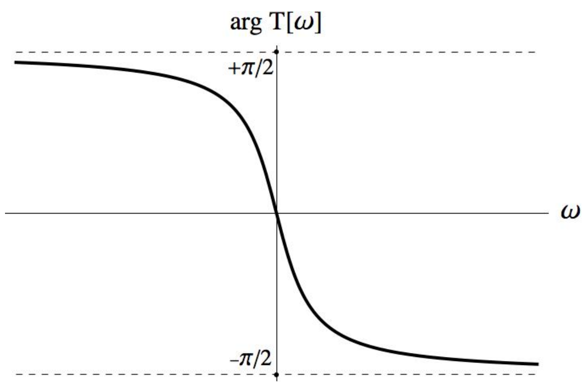

FIGURE 4. Phase shift as a function of signal frequency.

For low frequencies $|\omega|$ the phase-shift in the output signal is small, obviously because the population has enough time to react to the changing input. Large phase-shifts of maximally $\pm\pi/2$ occur at high frequencies of the input signal.

Since low-pass filters suppress high frequencies, the response x to a given input θ is smoother than the input itself (see figure below). This smoothing effect of the population is also immediately apparent from equation (6), reproduced here in terms of x and θ,

$$x(t) - \bar{x} = \partial_\theta f(\bar{x}, \bar{\theta}) \int_{-\infty}^{t} (\theta(\tau) - \bar{\theta}) e^{(t-\tau)\partial_x f(\bar{x}, \bar{\theta})} d\tau \tag{17}$$

It follows that whenever the input η is bounded and integrable (but not necessarily differentiable or even continuous), the output ξ is nonetheless always continuous or even differentiable.

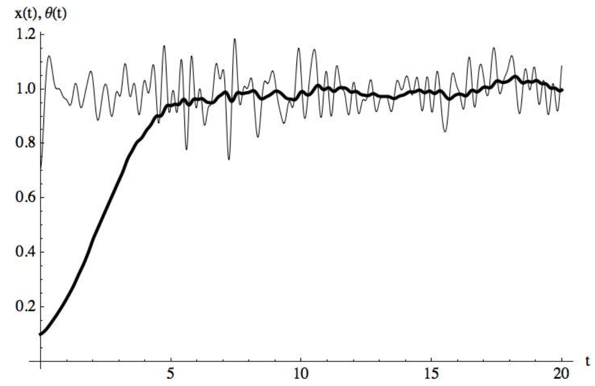

FIGURE 5. The smoothing effect of a low-pass filter.

2.3. **The logistic equation.** We apply the above to the logistic equation

$$\frac{dx}{dt} = f(x,\theta) = r(\theta)x\left(1 - \frac{x}{K(\theta)}\right). \tag{18}$$

For constant $\theta = \overline{\theta}$ with $r(\overline{\theta}) > 0$, we have $\overline{x} = K(\overline{\theta}) > 0$ is stable. Expression (8), for the transfer function, then gives

$$T(\omega) = \frac{r(\overline{\theta})K'(\overline{\theta})}{i\omega + r(\overline{\theta})}, \tag{19}$$

so that for the maximum gain we get

$$G_{\mathrm{m}} = |K'(\overline{\theta})|, \tag{20}$$

for the cutoff frequency

$$\omega_{\mathrm{c}} = r(\overline{\theta}) \tag{21}$$

and for the frequency-dependent phase-shift

$$\arg T(\omega) = -\arctan\frac{\omega}{r(\overline{\theta})} \tag{22}$$

Let θ be the birthrate in the mechanism underpinning the logistic equation as introduced in, respectively, sections 1.8 and 1.9. That is, we take $\theta = b$ for the mechanism in section 1.8 and $\theta = \alpha$ for the mechanism in section 1.9. For comparison, the following table gives the maximum gain, cut-off frequency and frequency-dependent phase-shift in terms of the model parameters.

	$\overline{\theta} = b$ (section 1.8)	$\overline{\theta} = \alpha$ (section 1.9)
G_m	$\frac{2}{c}$	$\frac{\gamma\delta}{\beta\overline{\theta}^2}$
ω_c	$\overline{\theta} - d$	$\frac{\beta e_0}{\delta}\overline{\theta} - \gamma$
$\arg T(\omega)$	$-\arctan\frac{\omega}{\overline{\theta}-d}$	$-\arctan\frac{\omega}{\frac{\beta e_0}{\delta}\overline{\theta}-\gamma}$

The following figure shows how the maximum gain and the cut-off frequency depend on the value of the average birthrate $\overline{\theta}$. In particular, notice how the G_m reacts differently to changes in average birth rate, depending on the underpinning mechanism.

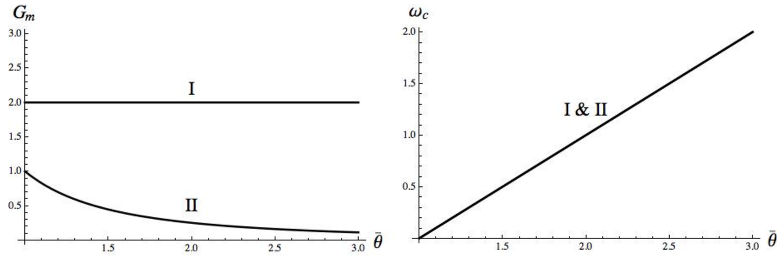

FIGURE 6. Response of the population filter characteristics G_m and ω_c to changes in the average birth rate $\overline{\theta}$ in mechanism I (section 1.8) and mechanism II (section 1.9).

A comparison of the effects of the death rates is more complicated, because the different underlying mechanism incorporate different kinds of mortality: in section 1.8 individuals die randomly at a rate d and because of contests at a rate c, while in section 1.9 individuals die as plants or seed at the rates γ and δ, respectively. Ignoring these differences and referring to all of them simply as "death rates", we observe from the table that in the mechanism of section 1.8 both the maximum gain and the cut-off frequency decrease as a function of the death rates, whereas in mechanism of section 1.9 only bandwidth decreases, while the maximum gain in fact *increases* as a function of the death rates.

This illustrates that a mechanistic underpinning of a model is necessary not only to be able to meaningfully vary different model parameters, but also that different mechanisms can give qualitatively different responses to changes in how the population reacts to fluctuating parameters.