STOCHASTIC POPULATION MODELS
(SPRING 2011)

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2. Fluctuating parameters

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

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

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

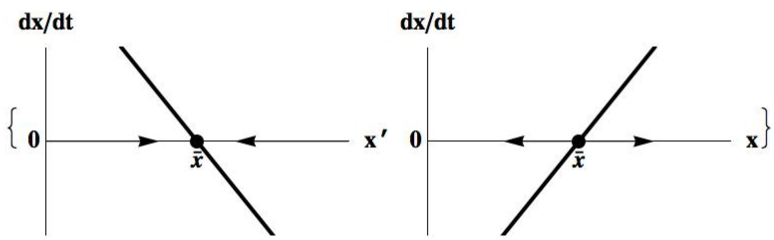

Figure 1. Stability and instability of $\bar{x}$ depending on the slope of $f(x, \bar{\theta})$.

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

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

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 this 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 $\partial_x f(\bar{x},\bar{\theta}) < 0$, 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 rest, i.e., the persistent solution,

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

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 now becomes clear: (1) $|T(\omega)|$ 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, and (2) $\arg T(\omega)$ 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 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.

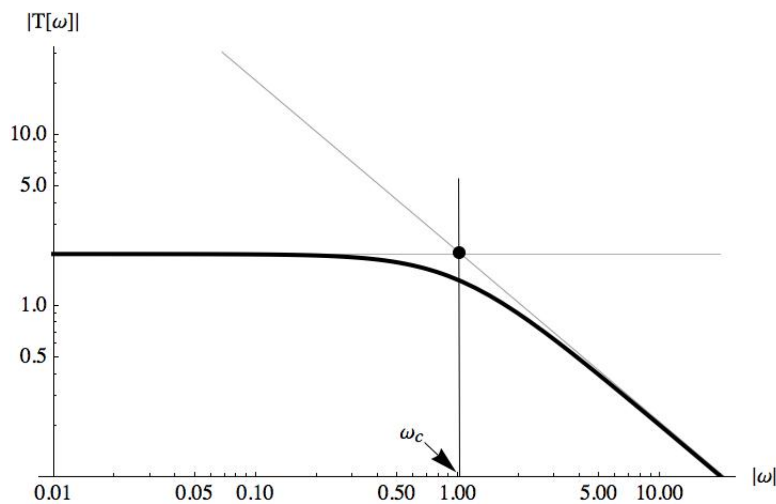

FIGURE 2. The gain as a function of signal frequency.

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.

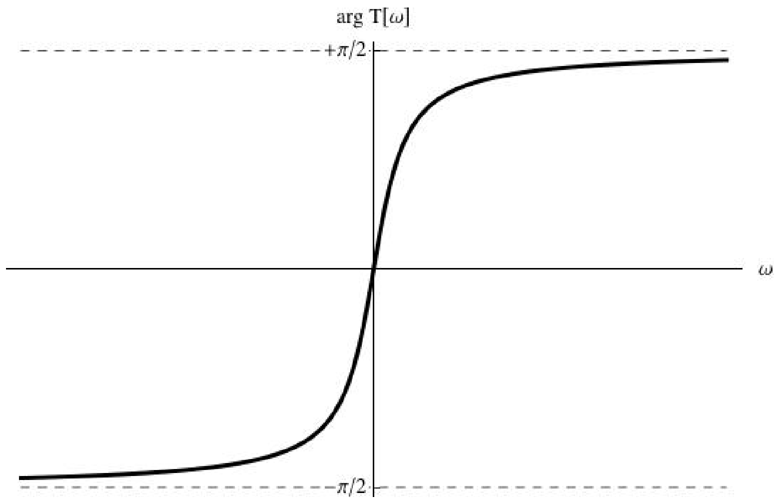

FIGURE 3. Phase shift as a function of signal frequency.

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 filter suppress high frequencies, the response x to an given input θ is smoother than the input itself (see figure below). This smoothing effect of the population is also immediately apparent from equation (5), 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 continuous and even differentiable.

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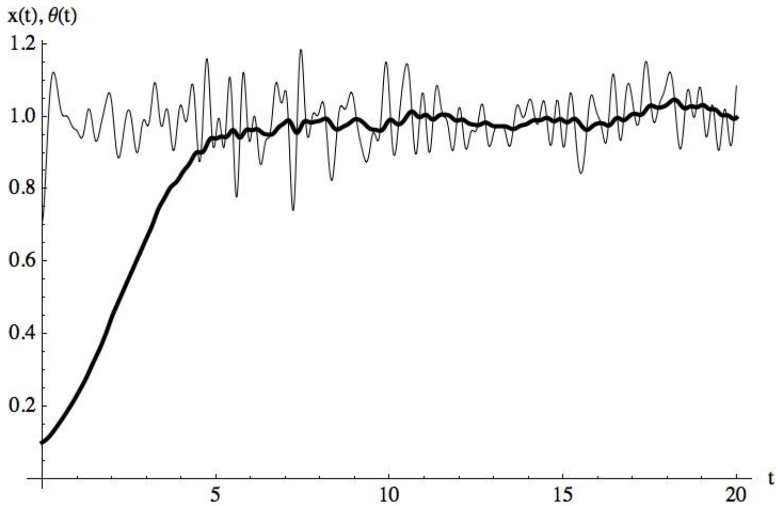

FIGURE 4. The smoothing effect of a low-pass filter.

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

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) \tag{18}$$

with

$$\begin{cases} r &= b - d \\ K &= 2(b-d)/c \end{cases} \tag{19}$$

(i.e., we use the mechanistic underpinning from section 1.8), and suppose that the birth rate b fluctuates around its average value $\bar{b}$ while the other parameters remain constant. How will this affect the population density?

In terms of equation (1) we have

$$\frac{dx}{dt} = f(x,b) := (b-d)x\left(1 - \frac{cx}{2(b-d)}\right) \tag{20}$$

If b is fixed at $\bar{b}$, then there is a stable equilibrium

$$\bar{x} = 2(\bar{b} - d)/c \tag{21}$$

Expression (8), for the transfer function, then gives

$$T(\omega) = \frac{2(\bar{b}-d)/c}{i\omega + \bar{b} - d} \tag{22}$$

Hence the gain is given by

$$|T(\omega)| = \frac{2|\bar{b}-d|/c}{\sqrt{\omega^2 + (\bar{b}-d)^2}} \tag{23}$$

so that the maximum gain is

$$G_{\mathrm{m}} = 2/c \tag{24}$$

and cutoff frequency is

$$\omega_{\mathrm{c}} = |\bar{b} - d| \tag{25}$$

The phase-shift is given by

$$\arg T(\omega) = -\arctan\left(\frac{\omega}{\bar{b} - d}\right) \tag{26}$$

Note that maximum gain is independent of the average birth rate and the death rate, and that the bandwidth (as characterized by the cutoff frequency) is independent of the contest rate c. The phase-shift, too, is independent of c.

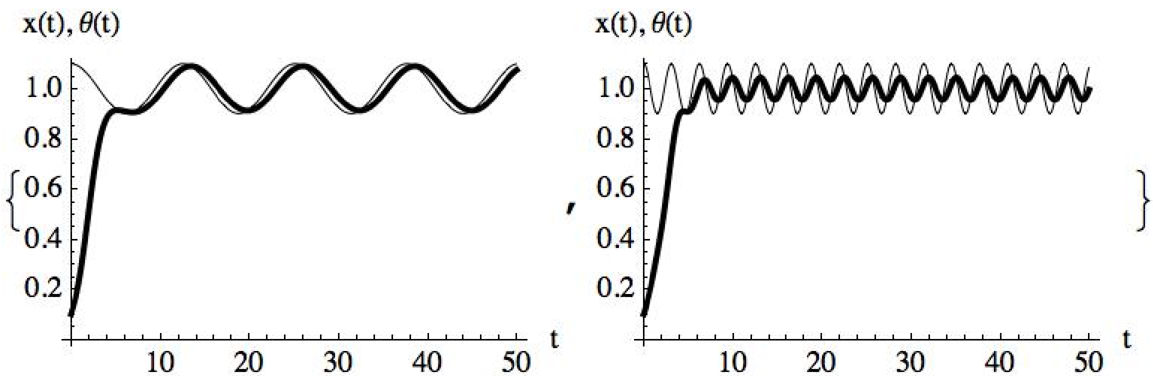

FIGURE 5. Gain and phase-shift in the response (bold lines) to inputs (thin lines) with different frequencies but the same amplitude.

2.4. **The logistic equation – II.** Now consider the logistic equation

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) \tag{27}$$

with

$$\begin{cases} r &= \frac{\alpha\beta e_0}{\delta} - \gamma \\ K &= e_0 - \frac{\gamma\delta}{\alpha\beta} \end{cases} \tag{28}$$

(i.e., we use the mechanistic underpinning presented in section 1.9), and suppose that the birth rate α fluctuates around its average value $\bar{\alpha}$ while the other parameters are remain constant. How will this affect the population, especially in comparison with the results of the previous section directly above?

If α is fixed at $\bar{\alpha}$, there is a stable equilibrium

$$\bar{x} = e_0 - \frac{\gamma\delta}{\bar{\alpha}\beta} \tag{29}$$

For the transfer function we get

$$T(\omega) = \frac{\gamma\delta\left(\frac{\bar{\alpha}\beta e_0}{\delta} - \gamma\right)}{\bar{\alpha}^2\beta\left(i\omega + \frac{\bar{\alpha}\beta e_0}{\delta} - \gamma\right)} \tag{30}$$

The gain then becomes

$$|T(\omega)| = \frac{\gamma\delta\left|\frac{\bar{\alpha}\beta e_0}{\delta} - \gamma\right|}{\bar{\alpha}^2\beta\sqrt{\omega^2 + \left(\frac{\bar{\alpha}\beta e_0}{\delta} - \gamma\right)^2}} \tag{31}$$

with a maximum gain

$$G_{\mathrm{m}} = \frac{\gamma\delta}{\bar{\alpha}^2\beta} \tag{32}$$

and cutoff frequency

$$\omega_{\mathrm{c}} = \left|\frac{\bar{\alpha}\beta e_0}{\delta} - \gamma\right| \tag{33}$$

Note that while in the previous section the maximum gain does not depend on the average birth rate at all, in the present section the maximum gain rapidly decreases as the inverse of the square of the average birth rate. The bandwidth, i.e., the cutoff frequency, increases with the average birth rate for both cases.

A comparison of the effects of the dearth rates is a bit more complicated, because the different underlying mechanism incorporate different kinds of mortality: in the previous section individuals die randomly at a rate d and because of contests at a rate c, while in the present section 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 that in the previous section both the maximum gain and the bandwidth decrease as a function of the death rates, whereas in the present section 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 (see section 1.10), but also that different mechanisms can give qualitatively different responses to changes in how the population reacts to fluctuating parameters.