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Mark Rees and Stephen P. Ellner. 2009. Integral projection models for populations in temporally varying environments. *Ecological Monographs* 79:575–594.

Appendix F. Perturbations to vital rate functions.

As a first simple example, consider the elasticity to the size-dependent survival function in a kernel of the form

$$K(y,x;\theta)=s(x;\theta)g(y,x)+B(x,\theta)\,f_d(y)\,. \tag{F.1}$$

Here B represents the net fecundity (including establishment probability) for a size x individual, and f_d is the offspring size distribution. In this Appendix only, to simplify notation we write $s(x,\theta)$ for the size-dependent survival instead of $p_s(x)$. Our *Carlina* model does not have this form because the fatality of flowering creates an interaction between reproduction and survival. To compute the overall elasticity of λ_S to survival at all sizes we use a proportional perturbation, i.e. $s(x,\theta)$ is perturbed to $s(x,\theta)+\varepsilon s(x,\theta)$. This perturbs the kernel (F.1) to $K(y,x;\theta)+\varepsilon s(x;\theta)g(y,x)$, so the elasticity is therefore given by equation (10) with $C_t(y,x)=s(x;\theta_t)g(y,x)$. For elasticity to the mean survival the perturbation kernel is $C_t(y,x)=\overline{s}(x)g(y,x)$ and again equation (10) applies.

The effect of perturbing the variability in s depends on the pattern of variability in the unperturbed kernel. If s is time-varying, then the elasticity of λ_S to the standard deviation of s is the difference between the overall elasticity and the elasticity to the mean. If s is time-invariant, then the elasticity to variability is by definition zero. To compute the sensitivity to added variance we perturb $s(x,\theta_t)$ to $s(x,\theta_t)+\varepsilon z_t$ where z_t is a white-noise process with mean 0, variance 1. The corresponding perturbation kernel is $H_t(y,x)=z_t g(y,x)$. Because this H has zero mean and is independent of the unperturbed kernel (as a consequence of g being time-invariant), the sensitivity of λ_S to the variance in s is therefore computed using equation (12), giving after some algebra $-\dfrac{\lambda_S}{2}E\left[\dfrac{\langle v_{t+1,}g(y,x)w_t\rangle^2}{\langle v_{t+1},K_t w_t\rangle^2}\right]$.

To compute the elasticity with respect to survival at a particular size x_0 we perturb $s(x,\theta)$ to $s(x,\theta)+\varepsilon s(x_0,\theta)\delta_{r,x_0}(x)$. The corresponding perturbation kernel is $C_t(y,x)=s(x_0,\theta)\delta_{r,x_0}(x)g(y,x)$, and letting $r\to 0$ in equation (10) the result is

$$E\left[s(x_0,\theta_t)w_t(x_0)\frac{\langle v_{t+1},g(y,x_0)\rangle}{\langle v_{t+1},K_t w_t\rangle}\right]. \tag{F.2}$$

For elasticity with respect to mean survival at size x_0 the perturbation to s is $\varepsilon\bar{s}(x_0)\delta_{r,x_0}(x)$, giving elasticity

$$\bar{s}(x_0)E\left[w_t(x_0)\frac{\langle v_{t+1},g(y,x_0)\rangle}{\langle v_{t+1},K_t w_t\rangle}\right] \tag{F.3}$$

As usual, the response to added variability in survival at size x_0 depends on the pattern of variability in the unperturbed kernel. If survival at size x_0 is time-varying, the elasticity of λ_S to the standard deviation of $s(x_0,\theta_t)$ is the difference between (F.3) and (F.2). If survival at size x_0 is time-invariant then (as usual) the elasticity and sensitivity to the standard deviation of added variance are zero. To compute the sensitivity to the variance of added variability, we perturb $s(x,\theta_t)$ to $s(x,\theta_t)+\varepsilon z_t\delta_{r,x_0}(x)$, so the perturbation kernel is $H_t(y,x)=z_t\delta_{r,x_0}(x)g(y,x)$ and the sensitivity can be computed using (12), giving $-\frac{\lambda_S}{2}E\left[\frac{\langle v_{t+1,}g(y,x)w_t\rangle^2}{\langle v_{t+1},K_t w_t\rangle^2}\right]$

As a more complicated example, consider the elasticity to flowering probability at some size x_0 in our *Carlina* model

$$K(y,x,\theta)=s(x;\theta)\left[(1-p_f(x;\theta))g(y,x;\theta)+p_f(x;\theta)f_n(x;\theta)f_d(y;\theta)p_e(t)\right]. \qquad \text{(F.4)}$$

To compute the elasticity of λ_S to $p_f(x_0,\theta_t)$, we perturb $p_f(x,\theta_t)$ to

$p_f(x,\theta_t)+\varepsilon p_f(x_0,\theta_t)\delta_{r,x_0}(x)$. The kernel is then perturbed by

$\varepsilon p_f(x_0,\theta)\delta_{r,x_0}(x)s(x,\theta)\left(p_e(t)f_n(x,\theta)f_d(y,\theta)-g(y,x)\right)$, so the perturbation kernel is

$$C_t(y,x)=p_f(x_0,\theta)\delta_{r,x_0}(x)s(x,\theta)\left(p_e(t)f_n(x,\theta)f_d(y,\theta)-g(y,x)\right). \qquad \text{(F.5)}$$

Proceeding as above the elasticity of λ_S to $p_f(x_0,\theta_t)$ is

$$E\left[s(x_0,\theta_t)p_f(x_0,\theta_t)w_t(x_0)\frac{\langle v_{t+1},p_e(t)f_n(x_0,\theta_t)f_d(y,\theta_t))-g(y,x_0)\rangle}{\langle v_{t+1},K_t w_t\rangle}\right]. \qquad \text{(F.6)}$$

This is hardly beautiful, but easy to compute from one long run of the unperturbed model. The elasticity to the mean flowering probability at size x_0 is given by (F.6) with $\bar{p}_f(x_0)$ in place of $p_f(x_0,\theta_t)$, and the difference between (F.6) and the elasticity to the mean gives the elasticity to the standard deviation

As the examples illustrate, the possibilities are limited only by your imagination and your willingness to do algebra.