Environmental Stochasticity in IPMs

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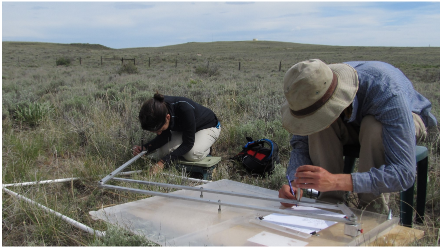


It's a noisy world

Long-lived adults	**Ratio**	**Diapausing seeds/eggs**	**Ratio**
Forest perennial plants	333	Chalk grassland annuals	1150
Desert perennial plants	4	Chapparal perennials	614
Marine inverebrates	591	Freshwater zooplankton	1150
Freshwater fish	706	Insects	31,600
Terrestrial vertebrates	38		
Birds	2200		

Hairston et al. (1996) compiled field studies that estimated per-capita reproductive success in a population in several different years at one location. For each, they computed the ratio between highest & lowest annual per-capita reproductive success omitting years when reproduction failed completely. Values shown are the highest ratio within each group.

Average vital rates don't tell the story

Simplest matrix/IPM with randomly varying rates:

$$N(t+1) = \lambda(t)N(t), N = \text{total number of individuals}$$

Suppose $\lambda(t) = 0.7$ or 1.35 (equal probability) each year.

Average $\lambda = 1.025 \Rightarrow$ 2.5% increase each year.

$$\bar{N}(t) = \bar{\lambda}^t N(0) = (1.025)^t N(0)$$

Lets see what really happens...

500 replicates, for 250 years

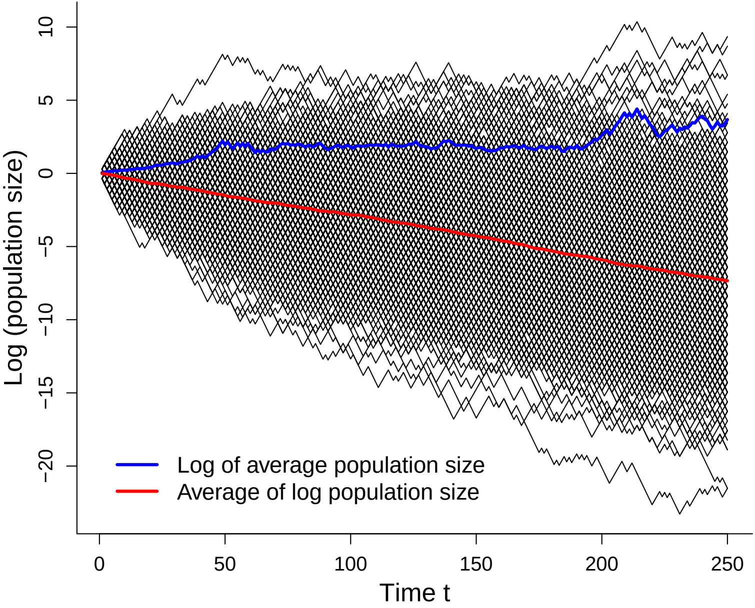
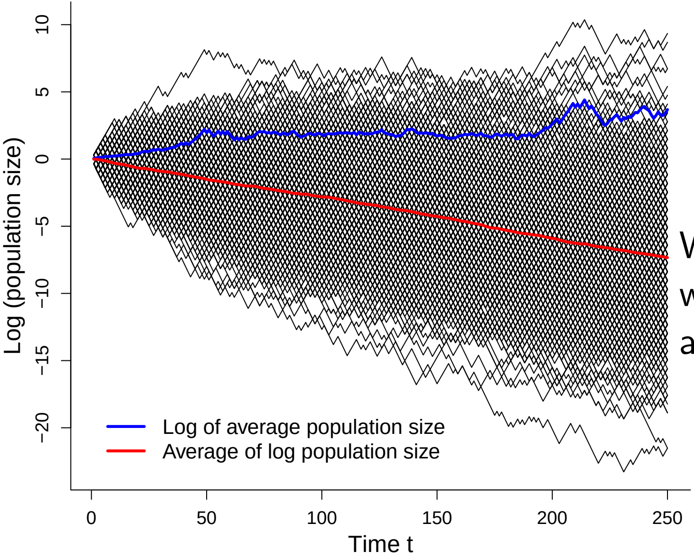


Figure produced by `RandomEnvironment1.R`

500 replicates, for 250 years



Which should we pay attention to?

Population size

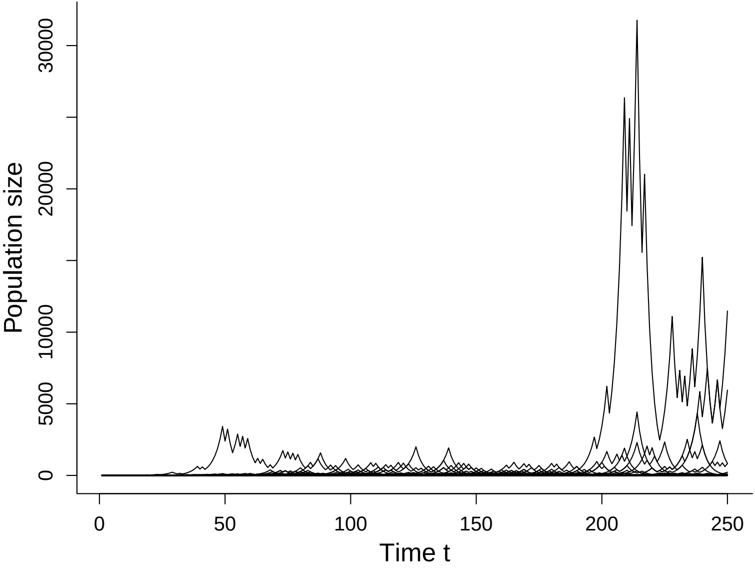


Figure produced by `RandomEnvironment1.R`

log(population size), 100 replicates for 2500 years

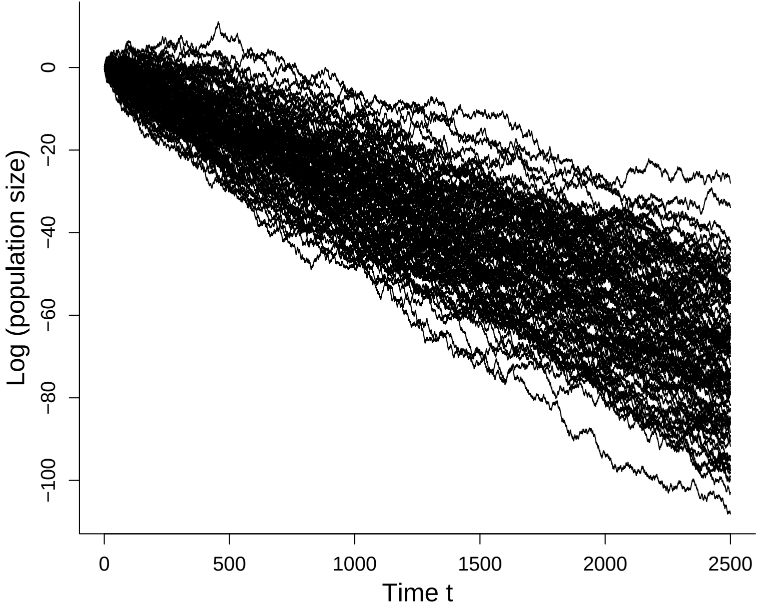


Figure produced by `RandomEnvironment1.R`

Let's do the math: unstructured population

$$\log N(t+1) = \log \lambda(t) + \log N(t)$$
$$x(t+1) = \rho(t) + x(t)$$

$$x(t) = x(0) + \rho(0) + \rho(1) + \cdots \rho(t-1)$$

Law of Large Numbers:

$$\frac{x(t)}{t} = \frac{\log N(t)}{t} \to \mathbb{E}[\rho] = \mathbb{E}[\log \lambda] \equiv \log \lambda_S$$

Central Limit Theorem:

$\log N(t) \approx$ Gaussian$\big(\mu = t \log \lambda_S, \sigma^2 = t\,\mathrm{Var}(\log \lambda)\big)$

Matrix models and IPMs: same story!

Density-independent matrix model or IPM $n(t+1) = K(t)n(t)$.

Suppose that

1. Environment is stationary – no trends over time.
2. No long-term correlations (technical: but independent, finite Markov chain are OK).
3. (IPMs) Each $K(z', z, t)$ is continuous in z and z'.
4. Positivity: there are constants $\alpha_1, \alpha_2 > 0$ such that for some $m > 0$,

$$\alpha_1 < K(m)K(m-1)K(m-2)\cdots K(1) < \alpha_2$$

with probability 1.

1. λ_S still exists

The long-term outcome is still exponential increase or decrease,

$$\frac{\log N(t)}{t} \to \log \lambda_S$$

where the long-term growth rate λ_S is non-random (same for every long-term projection) and $N(t)$ is any measure of total population size,

$$N(t) = \int W(z) n(z,t) dz.$$

2. λ_S can be computed

$$\log \lambda_S = \mathbb{E}\left[\log\left(\frac{N(t+1)}{N(t)}\right)\right]$$

Project for $t = 1, 2, \cdots, T$; compute one-step population growth

$$\lambda(t) = N(t+1)/N(t)$$

and average $\log \lambda(t)$ values.

There is no formula!

3. λ_S can be approximated

IPM version of Tuljapurkar's small-variance approximation

$$\log \lambda_S \approx \log \lambda_1 - \frac{Var\langle v, K_t w\rangle}{2\lambda_1^2} + \sum_{j=1}^{\infty} c_j.$$

- λ_1 =dominant eigenvalue of average kernel/matrix.
- v, w are dominant left, right eigenvectors of average kernel/matrix (reproductive value, stable distribution).
- c_j is effect of lag-k environmental correlations (0 if years are independent).

4. Perturbation analysis of λ_S

Sensitivity formula 1: Perturbing K_t to $K_t + \varepsilon C_t$

$$\frac{\partial \log \lambda_S}{\partial \varepsilon} = \frac{1}{\lambda_S}\frac{\partial \lambda_S}{\partial \varepsilon} = E\left[\frac{\langle v_{t+1}, C_t w_t\rangle}{\langle v_{t+1}, K_t w_t\rangle}\right]$$

Sensitivity formula 2: Perturbing K_t to $K_t + \varepsilon H_t$ where H_t has mean 0 and is independent of K_t

$$\frac{\partial \log \lambda_S}{\partial \varepsilon} = 0, \quad \frac{\partial \log \lambda_S}{\partial \varepsilon^2} = -\frac{1}{2}E\left[\frac{\langle v_{t+1}, H_t w_t\rangle^2}{\langle v_{t+1}, K_t w_t\rangle^2}\right].$$

w_0 arbitrary, iterate forward to $t = T$ (big).

$$\tilde{w}_{t+1} = K_t w_t,$$
$$w_{t+1} = \tilde{w}_{t+1} / \int \tilde{w}_{t+1}(z) dz$$

v_T arbitrary, iterate backwards to $t = 0$.

$$\tilde{v}_{t-1} = v_t K_{t-1} = \int v_t(z') K_{t-1}(z', z) dz',$$
$$v_{t-1} = \tilde{v}_{t-1} / \int \tilde{v}_{t-1}(z) dz$$

Compute averages over $t = t_b$ to $t = (T - t_b)$

Many possible perturbations!

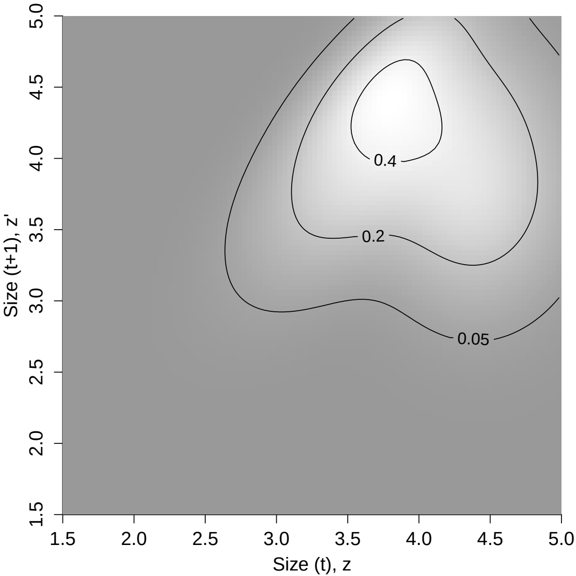
Tuljapurkar et al. (2003, 2004): if p_t is some time-varying part of the model, we can

- Perturb only the mean, leaving variance the same.
- Perturb only the variance, leaving the mean the same.
- Fractional perturbation (e.g., 5% higher value each year), which changes mean and variance.

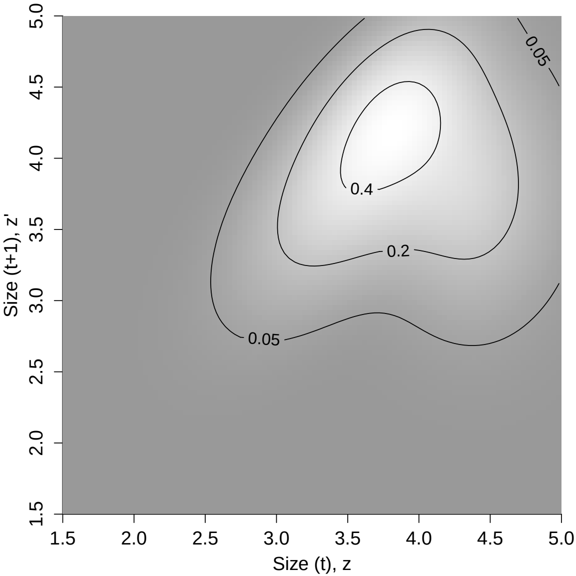
We can also add variance to a constant (not time-varying) part of the model.

Sensitivity measure	Notation and Formula
Sensitivity of λ_S to kernel value $K_t(z', z)$ = sensitivity of λ_S to mean of $K_t(z', z)$	$s_S(z', z) = s_S^{\mu}(z', z) = \lambda_S E\left[\frac{v_{t+1}(z')w_t(z)}{\langle v_{t+1}, K_t w_t\rangle}\right]$
Elasticity of λ_S to kernel value $K_t(z', z)$	$e_S(z', z) = E\left[\frac{v_{t+1}(z')w_t(z)K_t(z', z)}{\langle v_{t+1}, K_t w_t\rangle}\right]$
Elasticity of λ_S to the mean of kernel value $K_t(z', z)$	$e_S^{\mu}(z', z) = \bar{K}(z', z) E\left[\frac{v_{t+1}(z')w_t(z)}{\langle v_{t+1}, K_t w_t\rangle}\right]$
Elasticity to standard deviation of kernel value $K_t(z', z)$	$e_S^{\sigma}(z', z) = e_S(z', z) - e_S^{\mu}(z', z)$ $(= 0$ if $Var(K_t(z', z)) = 0)$
Sensitivity of λ_S to the standard deviation of time-varying kernel value $K_t(z', z)$	$s_S^{\sigma}(y, x) = \lambda_S e_S^{\sigma}(z', z)/\sqrt{Var(K_t(z', z)}$
Sensitivity of λ_S to the variance of time-varying kernel value $K_t(z', z)$	$s_S^{\sigma^2}(z', z) = 0.5 s_S^{\sigma}(z', z)/\sqrt{Var(K_t(z', z)}$
Sensitivity to adding independent variability to a time-invariant kernel value $K(z', z)$	$s_S^{\sigma^2,0}(z', z) = -\frac{\lambda_S}{2} E\left[\frac{(v_{i+1}(z')w_i(z))^2}{\langle v_{i+1}, K_i w_i\rangle^2}\right]$
Sensitivity of λ_S to parameter θ_i = sensitivity of λ_S to mean of θ_i	$s_{S,i} = s_{S,i}^{\mu} = \lambda_S E\left[\left\langle v_{t+1}, \frac{\partial K_t}{\partial \theta_i} w_t\right\rangle / \langle v_{t+1}, K_t w_t\rangle\right]$
Elasticity of λ_S to parameter θ_i	$e_{S,i} = E\left[\theta_i(t)\left\langle v_{t+1}, \frac{\partial K_t}{\partial \theta_i} w_t\right\rangle / \langle v_{t+1}, K_t w_t\rangle\right]$
Elasticity of λ_S to the mean of θ_i	$e_{S,i}^{\mu} = \bar{\theta}_i E\left[\left\langle v_{t+1}, \frac{\partial K_t}{\partial \theta_i} w_t\right\rangle / \langle v_{t+1}, K_t w_t\rangle\right]$
Elasticity of λ_S to the standard deviation of θ_i	$e_{S,i}^{\sigma} = e_{S,i} - e_{S,i}^{\mu}$ $[= 0$ if $Var(\theta_i) = 0]$
Sensitivity of λ_S to standard deviation of $\theta_i(t)$	$s_{S,i}^{\sigma} = \lambda_S e_{S,i}^{\sigma}/\sqrt{Var(\theta_i)}$
Sensitivity of λ_S to variance of $\theta_i(t)$	$s_{S,i}^{\sigma^2} = 0.5 s_{S,i}^{\sigma}/\sqrt{Var(\theta_i)}$
Sensitivity of λ_S to added variance in time-invariant parameter θ_i	$s_{S,i}^{\sigma^2,0} = \frac{\lambda_S}{2}\left(E\left[\left\langle v_{t+1}, \frac{\partial^2 K_t}{\partial \theta_i^2} w_t\right\rangle \Big/ \langle v_{t+1}, K_t w_t\rangle\right] - E\left[\left\langle v_{t+1}, \frac{\partial K_t}{\partial \theta_i} w_t\right\rangle^2 \Big/ \langle v_{t+1}, K_t w_t\rangle^2\right]\right)$

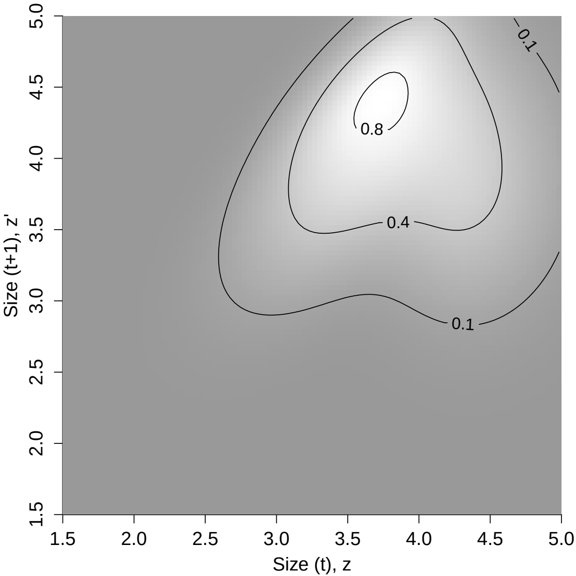
Carlina: Elasticity surface for mean kernel



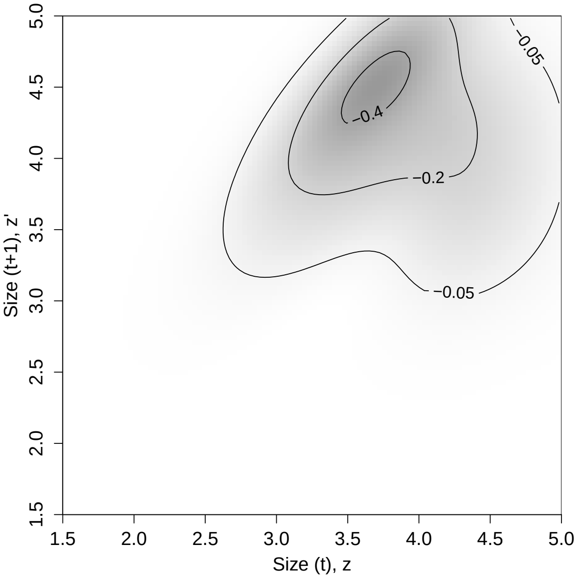
Carlina: Stochastic elasticity



Carlina: Stochastic elasticity to kernel mean



Carlina: Stochastic elasticity to kernel Std Dev



So, exactly how did I calculate those elasticities?

Let's take a look...

`Carlina Kernel Sampling K pert.R`

Distribution sampling

For IPMs, the alternative to kernel sampling is *distribution sampling.*

1. Instead of fitting a kernel for each year, estimate the probability distribution for the vector of parameters defining each year-specific kernel.
2. Simulate the model by sampling parameter vectors from that distribution.

This typically starts with fitting the demographic models in a random-effects framework.

Example: modeling survival as logistic regression with year-dependent slope and intercept

Fixed effects model

```
mod.Surv.fixed <- glm(Surv ~ z*Yeart, family = binomial,
                      data = sim.data)
cfixed <- coef(mod.Surv.fixed);
intercept.yr.fix <- cfixed[1]+c(0,cfixed[3:21]);
```

Random effects model, uncorrelated random effects

```
mod.Surv <- glmer(Surv ~ z + (1|Yeart) + (0 + z|Yeart),
               family = binomial, data = sim.data)
intercept.yr.re <- coef(mod.Surv)$Yeart[,1];
```

```
> summary(mod.Surv)
            .
            .
            .
Random effects:
 Groups  Name        Variance Std.Dev.
 Yeart   (Intercept) 0.9151   0.9566
 Yeart.1 z           0.1767   0.4204

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -2.5563     0.2738  -9.337   <2e-16 ***
z             0.9089     0.1083   8.392   <2e-16 ***
```

Intercept: Gaussian(mean=-2.5563, sd=0.9566)

Slope: Gaussian(mean=0.9089, sd=0.4204)

Demographic process	**Model**	**Parameter estimates**
Size dynamics: rosette growth and recruit size	$z' = a_0 + b_z z + \epsilon$ $z_R = a_R + \omega$	$b_z \sim N(0.74, 0.13)$ $\epsilon \sim N(0, 0.29)$ $\omega \sim N(0, 0.50)$ $a_0, a_R \sim MVN(\mu, \Sigma)$ $\mu = (1.14, 3.16)$ $\Sigma = \begin{pmatrix} 0.037 & 0.041 \\ 0.041 & 0.075 \end{pmatrix}$
Probability of survival	$\text{logit}(s(z)) = m_0 + m_z z$	$m_0 \sim N(-2.28, 1.16)$ $m_z \sim N(0.90, 0.41)$
Probability of flowering	$\text{logit}(p_b(z)) = \beta_0 + \beta_z z$	$\beta_0 \sim N(-16.19, 1.03)$ $\beta_z = 3.88$
Seed production	$b(z) = \exp(A{+}Bz)$	$A = 1$, $B = 2$

Correlations between different demographic models makes mixed-effects fitting *much* harder! Standard modeling functions (`lmer`, `glmer`, `gam`) are very limited. Instead, you need to fit all models simultaneously, in a Bayesian framework.

Correlations between different demographic models makes mixed-effects fitting *much* harder! Standard modeling functions (`lmer`, `glmer`, `gam`) are very limited. Instead, you need to fit all models simultaneously, in a Bayesian framework.

"At this point we strongly recommend you befriend a statistician or experienced JAGS user (chocolate, beer, lost puppy look – whatever it takes), as for the inexperienced these models can be tough and we all have, or know people who have, lost weeks/months failing to run JAGS models."

SPE, DZC and MR (2016), p. 201.

That's not good – because correlations are important.

So why not always do fixed-effects modeling and kernel sampling?

1. Between-year variance of fixed-effects parameter estimates includes true variability AND sampling error. Roughly,
   Estimated Variance = True Variance+Error Variance
2. Years with lower sample size (and less precise parameter estimates) count just as much as years with higher sample size.

That's not good, either. The whole point of mixed-effects modeling is to remove these problems.

Methods in Ecology and Evolution

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Statistical modelling of annual variation for inference on stochastic population dynamics using Integral Projection Models

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There are many options besides

1. Fixed-effects modeling and kernel sampling
2. Random-effects modeling and distribution sampling

We came up with 11.

We compared how well they estimated λ_S and Var($\lambda(t)$) from various amounts of simulated data, from Soay and monocarp individual-based models.

1. Correlations among parameters cannot be ignored.
2. Otherwise, everything sensible works about as well (i.e., about as badly).
3. λ_S: all cleverness is wasted. Do the simplest: fixed-effects models, kernel sampling.
4. Var($\lambda(t)$): (fixed-effects $+$ kernel sampling) is biased up; (mixed-effects $+$ kernel sampling), using BLUPS or posterior means, is biased down. So do both.

Because correlations matter, if they are present you should explore sensitivity to estimated correlations. *You can't do that with kernel sampling.*

1. Get year-specific parameters from fixed-effects or mixed-effects models of individual vital rates.
2. Compute the mean μ and variance-covariance matrix Σ of year-specific parameter vectors.
3. Do distribution sampling from multivariate Gaussian(μ, Σ).

See `Kernels to Distribution.R` for an example. Estimate covariance sensitivities numerically, by perturbing entries in Σ.