STOCHASTIC POPULATION MODELS (SPRING 2011)

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11. Multi-type processes

11.1. **The basic model.** Suppose that there are several types of individuals such as juveniles and adults, prey and predators, sick and heathy, hungry and satiated, and so forth. The number of individuals of each type then may change not just by birth and death, but also by maturation, infection, recovery, starvation, feeding and other processes.

As an example, let's only consider juveniles and adults where $I(t)$ denotes the number of juveniles and $J(t)$ the number of adults at time t. Changes in population composition are modeled as a stochastic process $\{(I(t), J(t))\}_{t\geq 0}$ on the set $\mathbb{N} \times \mathbb{N}$ of ordered pairs of the non-negative integers. Let further

$$P_{i,j}(t) := \mathrm{Prob}\{I(t) = i \text{ and } J(t) = j\} \tag{1}$$

denote the probability that at time t there are i juveniles and j adults. Four kinds of events may cause (i, j) to change over time, namely,

Event	Change
birth of a juvenile	$(i, j) \mapsto (i + 1, j)$
death of a juvenile	$(i, j) \mapsto (i - 1, j)$
death of an adult	$(i, j) \mapsto (i, j - 1)$
maturation of a juvenile	$(i, j) \mapsto (i - 1, j + 1)$

Assuming that birth, death and maturation are independent Poisson processes with rates $B_{i,j}$, $D^{\mathrm{j}}_{i,j}$, $M_{i,j}$ and $D^{\mathrm{a}}_{i,j}$, we have (cf. section 8.1):

$$\begin{array}{lllll} \frac{d}{dt}P_{i,j} = & + B_{i-1,j}P_{i-1,j} & - B_{i,j}P_{i,j} & \leftarrow \text{birth of a juvenile} \\ & + D^{\mathrm{j}}_{i+1,j}P_{i+1,j} & - D^{\mathrm{j}}_{i,j}P_{i,j} & \leftarrow \text{death of a juvenile} \\ & + D^{\mathrm{a}}_{i,j+1}P_{i,j+1} & - D^{\mathrm{a}}_{i,j}P_{i,j} & \leftarrow \text{death of an adult} \\ & + M_{i+1,j-1}P_{i+1,j-1} & - M_{i,j}P_{i,j} & \leftarrow \text{maturation of a juvenile} \\ & \quad\uparrow & \quad\uparrow & \\ & \text{Flow into } (i,j) & \text{Flow out of } (i,j) & \end{array} \tag{2}$$

11.2. **Semi-large systems approximation.** We use a similar change of variables as in section 9.1, i.e.,

$$
(3)\qquad \begin{cases} \varepsilon := & \Omega^{-1} & \text{(one over system size)} \\ x := & i\varepsilon & \text{(juvenile population density)} \\ y := & j\varepsilon & \text{(adult population density)} \\ p(t,x,y) := & P_{i,j}(t)/\varepsilon^2 & \text{(probability density)} \\ b(x,y)/y := & B_{i,j}/j & \text{(\textit{per capita} birth rate)} \\ d^{\mathrm{j}}(x,y)/x := & D^{\mathrm{j}}_{i,j}/i & \text{(\textit{per capita} juvenile death rate)} \\ d^{\mathrm{a}}(x,y)/y := & D^{\mathrm{a}}_{i,j}/j & \text{(\textit{per capita} adult rate)} \\ m(x,y)/x := & M_{i,j}/j & \text{(\textit{per capita} maturation rate)} \end{cases}
$$

Rewriting equation (2) in terms of the new variables gives

$$
(4)\qquad \begin{aligned} \varepsilon\,\partial_t p(x,y) = \; & +b(x-\varepsilon,y)\,p(x-\varepsilon,y) && -b(x,y)\,p(x,y) \\ & +d^{\mathrm{j}}(x+\varepsilon,y)\,p(x+\varepsilon,y) && -d^{\mathrm{j}}(x,y)\,p(x,y) \\ & +d^{\mathrm{a}}(x,y+\varepsilon)\,p(x,y+\varepsilon) && -d^{\mathrm{a}}(x,y)\,p(x,y) \\ & +m(x+\varepsilon,y-\varepsilon)\,p(x+\varepsilon,y-\varepsilon) && -m(x,y)\,p(x,y) \end{aligned}
$$

Second-order Taylor expansion of the right hand side leads to

$$
(5)\qquad \begin{aligned} \partial_t p = \; & -\partial_x(b-d^{\mathrm{j}}-m)p - \partial_y(-d^{\mathrm{a}}+m)p \\ & +\tfrac{\varepsilon}{2}\Big(\partial_x^2(b+d^{\mathrm{j}}+m)p + 2\partial_{xy}(-mp) + \partial_y^2(d^{\mathrm{a}}+m)p\Big) \end{aligned}
$$

which is a gives the Fokker-Plack equation. We shall now show that this can be written more generally (i.e., independently of the particular processes that are involved) as

$$
(6)\qquad \begin{aligned} \partial_t p = \; & -\partial_x\left[\tfrac{\mathcal{E}\{dx\}}{dt}p\right] - \partial_y\left[\tfrac{\mathcal{E}\{dy\}}{dt}p\right] \\ & +\tfrac{1}{2}\partial_x^2\left[\tfrac{\mathcal{E}\{dx^2\}}{dt}p\right] + \partial_{xy}\left[\tfrac{\mathcal{E}\{dxdy\}}{dt}p\right] + \tfrac{1}{2}\partial_y^2\left[\tfrac{\mathcal{E}\{dy^2\}}{dt}p\right] \end{aligned}
$$

where $\mathcal{E}\{dx\}/dt$ and $\mathcal{E}\{dy\}/dt$ are the expected changes dx and dy per unit of time in the population densities x and y, and $\mathcal{E}\{dx^2\}/dt$ and $\mathcal{E}\{dy^2\}/dt$ the variance of dx and dy per unit of time, and $\mathcal{E}\{dxdy\}/dt$ the covariance between dx and dy per unit of time.

To convince you that this is indeed so, consider the following table, which lists for each kind of event the accompanying change Δx and Δy together with the probability for the occurrence of each event within a Δt time interval.

Event	Δx	Δy	Probability
birth	$+\varepsilon$	0	$(b\,/\varepsilon)\Delta t + \mathrm{O}(\Delta t^2)$
juv. death	$-\varepsilon$	0	$(d^{\mathrm{j}}/\varepsilon)\Delta t + \mathrm{O}(\Delta t^2)$
adt. death	0	$-\varepsilon$	$(d^{\mathrm{a}}/\varepsilon)\Delta t + \mathrm{O}(\Delta t^2)$
maturation	$-\varepsilon$	$+\varepsilon$	$(m/\varepsilon)\Delta t + \mathrm{O}(\Delta t^2)$

From this table we can calculate the expected values

$$
(7)\qquad \begin{aligned} \mathcal{E}\{\Delta x\} = \; & (b-d^{\mathrm{j}}-m)\Delta t && +\mathrm{O}(\Delta t^2) \\ \mathcal{E}\{\Delta y\} = \; & (-d^{\mathrm{a}}+m)\Delta t && +\mathrm{O}(\Delta t^2) \end{aligned}
$$

and the (co-)variances

$$
\begin{aligned}
\mathcal{E}\{\Delta x^2\} &= \varepsilon(b+d^{\mathrm{j}}+m)\Delta t &+\mathrm{O}(\Delta t^2)\\
\mathcal{E}\{\Delta y^2\} &= \varepsilon(d^{\mathrm{a}}+m)\Delta t &+\mathrm{O}(\Delta t^2)\\
\mathcal{E}\{\Delta x\Delta y\} &= -\varepsilon\, m\,\Delta t &+\mathrm{O}(\Delta t^2)
\end{aligned} \tag{8}
$$

Division by Δt and letting $\Delta t \to 0$ gives expressions for expectations and (co-)variances of the infinitesimal changes dx and dy per unit of time, which on substitution into equation (6) give the Fokker-Planck equation (5).

The above can be generalized to any finite number of types of individuals with population densities $x_1, \dots, x_k$ and any number of processes as the Fokker-Plack equation

$$
\partial_t p = -\sum_{i=1}^{k} \partial_{x_i}\left[\frac{\mathcal{E}\{dx_i\}}{dt}p\right] + \frac{1}{2}\sum_{i,j=1}^{k} \partial_{x_i,x_j}\left[\frac{\mathcal{E}\{dx_i dx_j\}}{dt}p\right] \tag{9}
$$

With $\mathbf{x} := (x_1, \dots, x_k)$ and

$$
\mu(\mathbf{x}) := \left(\frac{\mathcal{E}\{dx_i\}}{dt}\right)_{i=1,\dots,k} \qquad (\text{“drift vector”}) \tag{10}
$$

and

$$
\sigma_\varepsilon^2(\mathbf{x}) := \left(\frac{\mathcal{E}\{dx_i dx_j\}}{dt}\right)_{i,j=1,\dots,k} \qquad (\text{“covariance matrix”}) \tag{11}
$$

and $\mathbf{W} := (dW_1, \dots, dW_k)$ as a vector of independent Wiener processes, the above Fokker-Planck equation corresponds to the multi-dimensional stochastic differential equation

$$
d\mathbf{x} = \mu(\mathbf{x})\,dt + \sigma_\varepsilon(\mathbf{x})\,d\mathbf{W} \quad (\text{Ito}) \tag{12}
$$

where $\sigma_\varepsilon = \sqrt{\sigma_\varepsilon^2}$ is the unique positive square root of the matrix σ_ε^2, which exists, because σ_ε^2 is symmetric and positive definite.

11.3. **Stationary distribution for semi-large systems.** Consider the multi-dimensional SDE

$$
d\mathbf{x} = \mu(\mathbf{x})\,dt + \sigma_\varepsilon(\mathbf{x})\,d\mathbf{W} \quad (\text{Ito}) \tag{13}
$$

and suppose $\bar{\mathbf{x}}$ is a deterministic equilibrium, i.e.,

$$
\mu(\bar{\mathbf{x}}) = \mathbf{0} \tag{14}
$$

and suppose further that $\bar{\mathbf{x}}$ is deterministically stable, i.e., all eigenvalues of the Jacobi matrix

$$
\mu'(\bar{\mathbf{x}}) := \left.\left(\partial_{x_i}\frac{\mathcal{E}\{dx_j\}}{dt}\right)_{i,j=1,\dots,k}\right|_{\mathbf{x}=\bar{\mathbf{x}}} \tag{15}
$$

have a strictly negative real part. We approximate the (generally) non-linear SDE (13) with the linear SDE

$$
d\mathbf{x} = \mu'(\bar{\mathbf{x}})(\mathbf{x}-\bar{\mathbf{x}})\,dt + \sigma_\varepsilon(\bar{\mathbf{x}})\,d\mathbf{W} \tag{16}
$$

which is the multi-dimensional Ornstein-Uhlenbeck process. Hence,

$$\lim_{t\to\infty} \mathbf{x}(t) \sim \mathcal{N}\big(\bar{\mathbf{x}}, \mathbf{C}_{\mathbf{x}}(0)\big) \tag{17}$$

which is the multi-normal distribution with mean $\bar{\mathbf{x}}$ and covariance matrix $\mathbf{C}_{\mathbf{x}}(0)$, i.e., the auto-covariance matrix $\mathbf{C}_{\mathbf{x}}(\tau)$ evaluated at $\tau = 0$.

The auto-covariance matrix for two stationary vector-values processes $\{\mathbf{u}(t)\}$ and $\{\mathbf{v}(t)\}$ with zero mean is defined as

$$\mathbf{C}_{\mathbf{u},\mathbf{v}}(\tau) = \mathcal{E}\{\mathbf{u}(t+\tau)\mathbf{v}(t)^{\mathrm{T}}\} \tag{18}$$

If $\mathbf{u} = \mathbf{v}$, then we may also write

$$\mathbf{C}_{\mathbf{u},\mathbf{u}} = \mathbf{C}_{\mathbf{u}} \tag{19}$$

From the definition of the auto-covariance matrix one readily shows that if $\mathbf{w} = \mathbf{A}\mathbf{u} + \mathbf{B}\mathbf{v}$ for given square matrices $\mathbf{A}$ and $\mathbf{B}$, then

$$\mathbf{C}_{\mathbf{w},\mathbf{w}} = \mathbf{A}\mathbf{C}_{\mathbf{u},\mathbf{u}}\mathbf{A}^{\mathrm{T}} + \mathbf{A}\mathbf{C}_{\mathbf{u},\mathbf{v}}\mathbf{B}^{\mathrm{T}} + \mathbf{B}\mathbf{C}_{\mathbf{v},\mathbf{u}}\mathbf{A}^{\mathrm{T}} + \mathbf{B}\mathbf{C}_{\mathbf{v},\mathbf{v}}\mathbf{B}^{\mathrm{T}} \tag{20}$$

and

$$\mathbf{C}_{\mathbf{u}',\mathbf{u}'} = -\mathbf{C}''_{\mathbf{u}} \tag{21}$$

$$\mathbf{C}_{\mathbf{u}',\mathbf{u}} = +\mathbf{C}'_{\mathbf{u}} \tag{22}$$

$$\mathbf{C}_{\mathbf{u}\ ,\mathbf{u}'} = -\mathbf{C}'_{\mathbf{u}} \tag{23}$$

Applying the above to the linear SDE

$$d\mathbf{x} - \mu'(\bar{\mathbf{x}})(\mathbf{x} - \bar{\mathbf{x}})\,dt = \sigma_\varepsilon(\bar{\mathbf{x}})\,d\mathbf{W} \tag{24}$$

we get

$$-\mathbf{C}''_{\mathbf{u}} - \mathbf{C}'_{\mathbf{u}}\,\mu'(\bar{\mathbf{x}})^{\mathrm{T}} + \mu'(\bar{\mathbf{x}})\,\mathbf{C}'_{\mathbf{u}} + \mu'(\bar{\mathbf{x}})\,\mathbf{C}_{\mathbf{u}}\,\mu'(\bar{\mathbf{x}})^{\mathrm{T}} = \sigma^2_\varepsilon(\bar{\mathbf{x}})\,\delta_{\mathrm{Dirac}}\mathbf{I} \tag{25}$$

where δ_{Dirac} is the Dirac delta function and $\mathbf{I}$ is the identity matrix. Taking Fourier transforms gives an equation for the spectral density matrix $\mathbf{S}_{\mathbf{u}}$:

$$-(i\omega)^2\mathbf{S}_{\mathbf{u}} - i\omega\mathbf{S}_{\mathbf{u}}\,\mu'(\bar{\mathbf{x}})^{\mathrm{T}} + i\omega\mu'(\bar{\mathbf{x}})\,\mathbf{S}_{\mathbf{u}} + \mu'(\bar{\mathbf{x}})\,\mathbf{S}_{\mathbf{u}}\,\mu'(\bar{\mathbf{x}})^{\mathrm{T}} = \sigma^2_\varepsilon(\bar{\mathbf{x}}) \tag{26}$$

which can be rewritten as

$$\Big(\mu'(\bar{\mathbf{x}}) - i\omega\mathbf{I}\Big)\,\mathbf{S}_{\mathbf{u}}\,\Big(\mu'(\bar{\mathbf{x}}) + i\omega\mathbf{I}\Big)^{\mathrm{T}} = \sigma^2_\varepsilon(\bar{\mathbf{x}}) \tag{27}$$

and hence

$$\mathbf{S}_{\mathbf{u}}(\omega) = \Big(\mu'(\bar{\mathbf{x}}) - i\omega\mathbf{I}\Big)^{-1}\sigma^2_\varepsilon(\bar{\mathbf{x}})\,\Big(\mu'(\bar{\mathbf{x}}) + i\omega\mathbf{I}\Big)^{-\mathrm{T}} \tag{28}$$

(Note that since all eigenvalues of $\mu'(\bar{\mathbf{x}})$ are assumed to have a strictly negative real part, the inverses in above equations exist.) The auto-covariance matrix is then found by taking the component-wise inverse Fourier transform

$$\mathbf{C}_{\mathbf{u}}(\tau) = \frac{1}{2\pi}\int_{-\infty}^{\infty}\mathbf{S}_{\mathbf{u}}(\omega)e^{i\omega\tau}d\omega \tag{29}$$

In particular, the covariance matrix of the stationary distribution (17) is given by

$$\mathbf{C}_{\mathbf{x}}(0) = \mathbf{C}_{\mathbf{u}}(0) = \frac{1}{2\pi}\int_{-\infty}^{\infty}\mathbf{S}_{\mathbf{u}}(\omega)d\omega \tag{30}$$

11.4. **Example.** Consider an insect or fish population where the adults cannibalize the juveniles (or eggs) of their own species. Food is assumed to be not a limiting factor for offspring productions, and so the cannibalism does not increase fecundity. Let X denote a juvenile individual (or egg), and let Y denote an adult. The processes on the individual level are given by the following "reactions":

$$\begin{array}{rcll} \mathrm{Y} & \xrightarrow{\alpha} & \mathrm{Y}+\mathrm{X} & \text{(birth)} \\ \mathrm{X} & \xrightarrow{\beta} & \mathrm{Y} & \text{(maturation)} \\ \mathrm{Y}+\mathrm{X} & \xrightarrow{\gamma} & \mathrm{Y}+\dagger & \text{(death of juvenile by cannibalism)} \\ \mathrm{X} & \xrightarrow{\mu} & \dagger & \text{(death of juvenile by other causes)} \\ \mathrm{Y} & \xrightarrow{\nu} & \dagger & \text{(death of adult)} \end{array} \tag{31}$$

Applying the law of mass-action, the population equations are

$$\begin{cases} \frac{dx}{dt} = & b(x,y) - d^{\mathrm{j}}(x,y) - m(x,y) \quad \text{(juvenile)} \\ \frac{dy}{dt} = & m(x,y) - d^{\mathrm{a}}(x,y) \quad \text{(adult)} \end{cases} \tag{32}$$

where

$$\begin{cases} b(x,y) = & \alpha y & \text{(birth rate)} \\ d^{\mathrm{j}}(x,y) = & \gamma x y + \mu x & \text{(total juvenile death rate)} \\ d^{\mathrm{a}}(x,y) = & \nu y & \text{(adult death rate)} \\ m(x,y) = & \beta x & \text{(maturation rate)} \end{cases} \tag{33}$$

For the x-isocline we find

$$\frac{dx}{dt} = 0 \Longleftrightarrow y = \frac{(\beta+\mu)x}{\alpha - \gamma x} \tag{34}$$

and for the y-isocline we have

$$\frac{dy}{dt} = 0 \Longleftrightarrow y = \frac{\beta x}{\nu} \tag{35}$$

Depending on the relative size of the slopes of the isoclines near the origin, we distinguish two qualitatively different cases:

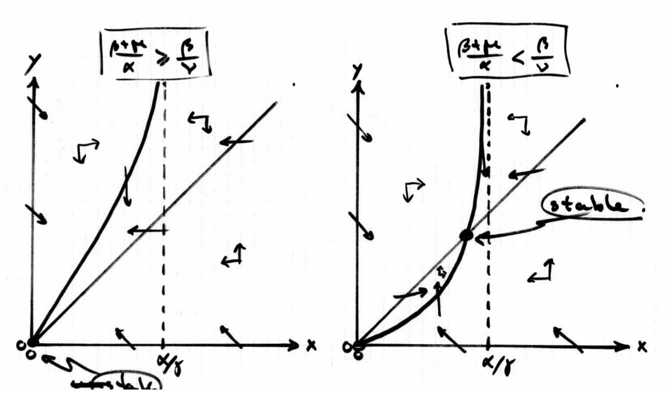

FIGURE 1. example caption

The case on the left ($(\beta+\mu)\alpha \geq \beta/\nu$) leads to rapid extinction and is not interesting for us. We focus on the second case ($(\beta+\mu)\alpha < \beta/\nu$) where there exists a globally stable positive equilibrium

$$\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix} = \begin{pmatrix} \frac{\alpha\beta-(\beta+\mu)\nu}{\beta\gamma} \\ \\ \frac{\alpha\beta-(\beta+\mu)\nu}{\gamma\nu} \end{pmatrix} \tag{36}$$

The non-linear stochastic differential equation (13) for semi-large systems is

$$d\begin{pmatrix} x \\ y \end{pmatrix} = \mu(x,y)\,dt + \sigma_\varepsilon(x,y)\,d\begin{pmatrix} W_1 \\ W_2 \end{pmatrix} \tag{37}$$

where

$$\mu(x,y) = \begin{pmatrix} b(x,y) - d^{\mathrm{j}}(x,y) - m(x,y) \\ -d^{\mathrm{a}}(x,y) + m(x,y) \end{pmatrix} \tag{38}$$

and

$$\sigma_\varepsilon^2(x,y) = \varepsilon \begin{pmatrix} b(x,y) + d^{\mathrm{j}}(x,y) + m(x,y) & -m(x,y) \\ -m(x,y) & d^{\mathrm{a}}(x,y) + m(x,y) \end{pmatrix} \tag{39}$$

And so the linear approximation (16) near the deterministic equilibrium $(\bar{x},\bar{y})$ becomes

$$d\begin{pmatrix} x \\ y \end{pmatrix} = \mu'(\bar{x},\bar{y}) \begin{pmatrix} x-\bar{x} \\ y-\bar{y} \end{pmatrix} dt + \sigma_\varepsilon(\bar{x},\bar{y})\,d\begin{pmatrix} W_1 \\ W_2 \end{pmatrix} \tag{40}$$

where

$$\mu'(\bar{x},\bar{y}) = \begin{pmatrix} -\beta-\mu-\gamma\bar{y} & \alpha-\gamma\bar{x} \\ \beta & -\nu \end{pmatrix} \tag{41}$$

is the Jacobi matrix (15) evaluated at the deterministic equilibrium $(\bar{x},\bar{y})$. System (40) has a stationary bi-bvariate normal distribution

$$\begin{pmatrix} x \\ y \end{pmatrix} \sim \mathcal{N}\left(\begin{pmatrix} \bar{x} \\ \bar{y} \end{pmatrix}, \mathbf{C}(0)\right) \tag{42}$$

The covariance matrix $\mathbf{C}(0)$ is found by first calculating the spectral density $\mathbf{S}(\omega)$ as in equation (28). From that, by a (numerical) inverse Fourier transform, we calculate the auto-covariance matrix $\mathbf{C}(\tau)$ as in equation (29), which for $\tau = 0$ gives us the covariance matrix $\mathbf{C}(0)$ of the stationary distribution.

The following numerical results were obtained for parameter values

$$\alpha = 10,\ \beta = 2,\ \gamma = 1,\ \mu = 1 \text{ and } \nu = 1$$

These values give an equilibrium with

$$\bar{x} = 8.5 \text{ and } \bar{y} = 17.0$$

With a system size of $\varepsilon^{-1} = 100$ this corresponds to 850 juveniles and 1700 adults in total. The autocovariance of the stationary distribution was found to be

$$\mathbf{C}(0) = \varepsilon \begin{pmatrix} 8.5 & 2.1 \\ 2.1 & 20 \end{pmatrix}$$

This means that the number juveniles varies about 99% of the time between the values $\varepsilon^{-1}(\bar{x} - 3\sqrt{\mathbf{C}_{11}(0)}) = 760$ and $\varepsilon^{-1}(\bar{x} + 3\sqrt{\mathbf{C}_{11}(0)}) = 940$. Likewise, the number of adults varies about 99% of the time between the values $\varepsilon^{-1}(\bar{y} - 3\sqrt{\mathbf{C}_{22}(0)}) = 1570$ and $\varepsilon^{-1}(\bar{x} + 3\sqrt{\mathbf{C}_{22}(0)}) = 1830$.

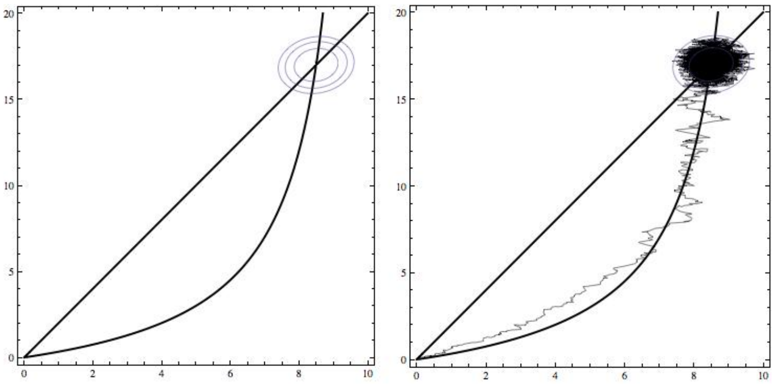

FIGURE 2. The figure on the left shows the phase plane with the population density x of juveniles along the horizontal axis and the population density of adults along the vertical axis. The deterministic equilibrium lies at the positive intersection of the isoclines (solid lines). The ovals are contour lines of the probability density of the stationary distribution including 90, 99 and 99.9 percent of the probability mass. The figure on the right shows the phase plane with a single sample path, i.e., a single realization of the non-linear SDE (37).

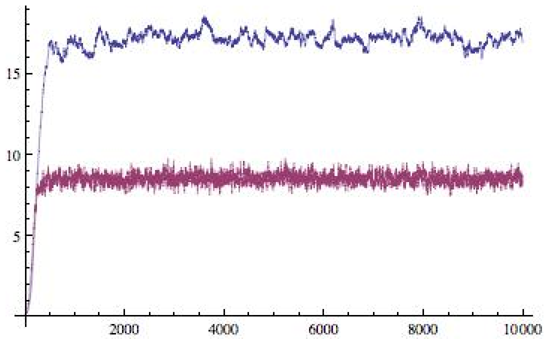

FIGURE 3. The population density of juveniles (bottom) and adults (top) from a single realization of the non-linear SDE (37) plotted as functions of time. The difference in the kind of fluctuations can be understood from the auto-covariance function (see next figure).

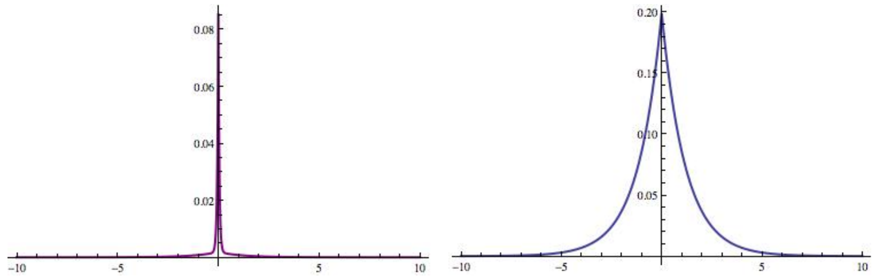

FIGURE 4. The auto-covariance function $\mathbf{C}_{11}(\tau)$ for juveniles (left) and the auto-covariance function $\mathbf{C}_{22}(\tau)$ for adults (right). It can be seen that the correlation across time extends much further for adults than for juveniles. This explains the faster, more erratic fluctuations for juveniles than for adults as seen in the previous figure.