STOCHASTIC POPULATION MODELS (SPRING 2011)

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6. Fluctuation statistics of stationary processes

6.1. **Mean and auto-covariance of a stochastic process.** Let $\{X(t)\}$ be a stochastic process. Then the mean of the process is defined as

$$\overline{X}(t) := \mathcal{E}\{X(t)\} \tag{1}$$

and the auto-covariance as

$$C_X(t_1, t_2) := \mathcal{E}\left\{\big(X(t_1) - \overline{X}(t_1)\big)\big(X(t_2) - \overline{X}(t_2)\big)\right\} \tag{2}$$

The auto-covariance gives the covariance between two different points in time. For example, take the Wiener process $\{W(t)\}$. Then from Section 5.3 we know that

$$\overline{W}(t) = 0 \tag{3}$$

and the auto-covariance as

$$C_W(t_1, t_2) = \mathcal{E}\{W(t_1)W(t_2)\} = \min\{t_1, t_2\} \tag{4}$$

6.2. **Stationary stochastic processes.** A stochastic process $\{X(t)\}$ is stationary if the probability distribution of $X(t)$ does not depend on t. For the Wiener process $\{W(t)\}$ we have

$$W(t) \sim \mathcal{N}(0, t) \tag{5}$$

in which the variance depends on t, and so the Wiener process is *not* stationary. However, for any fixed Δt the Wiener increment

$$\Delta W(t) := W(t + \Delta t) - W(t) \tag{6}$$

is distributed as

$$\Delta W(t) \sim \mathcal{N}(0, \Delta t) \tag{7}$$

which is independent of t, and so the process $\{\Delta W(t)\}$ is stationary.

For the Ornstein-Uhlenbeck process $\{X(t)\}$ with initial value $X(0) = x_0$ we found in Section 5.4 that

$$X(t) \sim \mathcal{N}\left(x_0 e^{-at}, \frac{b^2}{2a}\big(1 - e^{-2at}\big)\right) \tag{8}$$

(for positive a and b) which is obviously not stationary. However,

$$\lim_{t\to\infty} X(t) \sim \mathcal{N}\left(0, \frac{b^2}{2a}\right) \tag{9}$$

does not depend on t and therefore is stationary. In other words, the Ornstein-Uhlenbeck process is *asymptotically* stationary.

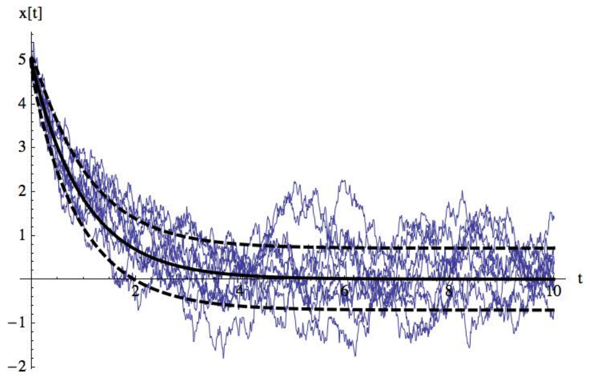

FIGURE 1. Ten sample paths of the Ornstein-Uhlenbeck process with $X(0) = 5$ and $a = b = 1$. Solid line indicates the mean and the dashed lines the mean plus/minus the standard deviation of the distribution of $X(t)$.

6.3. **Mean and auto-covariance of a stationary stochastic process.** The mean $\overline{X}$ of a stationary process $\{X(t)\}$ is independent of t, and the *auto-covariance*

$$C_X(\tau) := \mathcal{E}\left\{\left(X(t+\tau) - \overline{X}\right)\left(X(t) - \overline{X}\right)\right\} \tag{10}$$

depends only on the time-difference τ. One immediately verifies that the auto-covariance of a stationary process is an even function, i.e.,

$$C_X(\tau) = C_X(-\tau) \tag{11}$$

and that $C_X(0)$ is the variance of the process. We further introduce the *spectral density* of a stationary process as the Fourier transform of the auto-covarance, i.e.,

$$S_X(\omega) := \int_{-\infty}^{+\infty} C(\tau)e^{-i\omega\tau}d\tau \tag{12}$$

Note that since the auto-covariance is real and even, the spectral density is also a real and even function.

For the Wiener increment $\{\Delta W(t)\}$ over a time-interval of fixed length $\Delta t > 0$ we find by direct calculation that the mean

$$\overline{\Delta W} = 0 \tag{13}$$

and the auto-covariance

$$C_{\Delta W}(\tau) = \begin{cases} \Delta t - |\tau| & \text{if } |\tau| \le \Delta t \\ 0 & \text{otherwise} \end{cases} \tag{14}$$

and its Fourier transform, the spectral density

$$S_{\Delta W}(\omega) = \frac{2(1 - \cos \omega \Delta t)}{\omega^2} \tag{15}$$

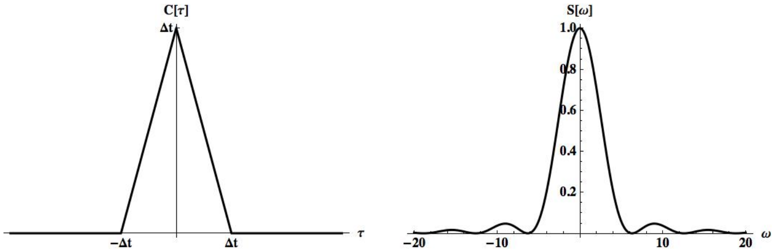

FIGURE 2. Auto-covariance and spectral density for the Wiener increment $\{\Delta W(t)\}$

In Section 5.5 we have seen that the Gaussian white noise is the stationary process $\{\xi(t)\}$ with $\mathcal{E}\{\xi(t)\} = 0$ and $\mathcal{E}\{\xi(t_1)\xi(t_2)\} = \delta(t_1 - t_2)$. The auto-covariance of the white noise therefore is

$$C_\xi(\tau) = \delta(\tau) \tag{16}$$

and the spectral density

$$S_\xi(\omega) = 1 \tag{17}$$

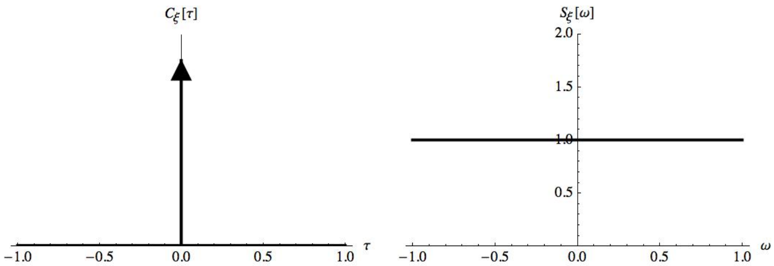

FIGURE 3. Auto-covariance and spectral density for the Gaussian white noise $\{\xi(t)\}$

6.4. **Useful properties of the auto-covariance and cross-covariance.** Consider the stationary Ornstein-Uhlenbeck process generated by the linear SDE

$$dX + aX\,dt = b\,dW \tag{18}$$

for positive a and b. How do we calculate the auto-covariance and spectral density of this process?

To answer this question we introduce the *cross-covariance* of two stationary processes $\{X(t)\}$ and $\{Y(t)\}$ as the function

$$C_{X,Y}(\tau) = \mathcal{E}\left\{\big(X(t+\tau) - \overline{X}\big)\big(Y(t) - \overline{Y}\big)\right\} \tag{19}$$

Notice that $C_{X,X}$ is identical to the auto-covariance C_X defined in Section 6.3, and $C_{X,Y}(0)$ is the covariance between $X(t)$ and $Y(t)$ for arbitrary t, and $C_{X,Y}(\tau) = C_{Y,X}(-\tau)$.

If, for arbitrary a and b, we define the process

$$Z(t) := aX(t) + bY(t) \tag{20}$$

then

$$C_{Z,Z} = a^2 C_{X,X} + abC_{X,Y} + abC_{Y,X} + b^2 C_{Y,Y} \tag{21}$$

Here are some further useful properties of the auto-covariance function:

(a) $C_{\frac{dX}{dt},Y} = +C'_{X,Y}$

(b) $C_{X,\frac{dY}{dt}} = -C'_{X,Y}$

(c) $C_{\frac{dX}{dt},\frac{dY}{dt}} = -C''_{X,Y}$

where $C'_{X,Y}$ and $C''_{X,Y}$ are the first- and second-order derivatives of $C_{X,Y}(\tau)$ with respect to τ. The proofs are left as an exercise. Applying these properties with $Y = X$ to the left and the right hand side of equation (18) gives

$$-C''_{X,X} + a^2 C_{X,X} = b^2 \delta \tag{22}$$

where δ is the Dirac delta distribution, which is the auto-covariance of the white noise dW/dt (see Section 6.3). This is a second-order differential equation that could be solved directly, but we can also take Fourier transforms, which gives

$$\omega^2 S_{X,X} + a^2 S_{X,X} = b^2 \tag{23}$$

It follows that spectral density of the stationary Ornstein-Uhlenbeck process is

$$S_{X,X}(\omega) = \frac{b^2}{\omega^2 + a^2} \tag{24}$$

Taking inverse Fourier transforms, we find that the auto-covariance is

$$C_{X,X}(\tau) = \frac{b^2}{2|a|} e^{-|a\tau|} \tag{25}$$

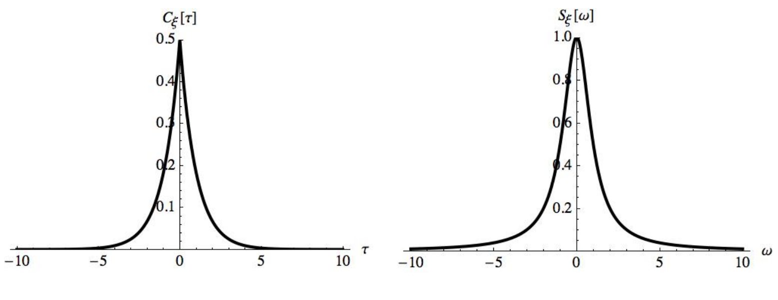

FIGURE 4. Auto-covariance and spectral density for the Ornstein-Uhlenbeck process (18) with $a = b = 1$.

6.5. **Linear second-order auto-correlative process.** Consider the *linear second-order auto-correlative process* given by the differential equation

$$\frac{d^2X}{dt^2} + a\frac{dX}{dt} + bX = c\frac{dW}{dt} \tag{26}$$

where dW/dt is the Gaussian white noise. The above equation is equivalent to the system of first-order linear stochastic differential equations

$$\begin{cases} dX = Y\,dt \\ \\ dY + aY\,dt + bX\,dt = dW \end{cases} \tag{27}$$

The corresponding homogeneous ordinary differential equation

$$\frac{d^2X}{dt^2} + a\frac{dX}{dt} + bX = 0 \tag{28}$$

has the following explicit solution:

$$X(t) = Ae^{-\frac{1}{2}t\left(a+\sqrt{a^2-4b}\right)} + Be^{-\frac{1}{2}t\left(a-\sqrt{a^2-4b}\right)} \tag{29}$$

for given constants A and B. It can be seen that for $a > 0$, the deterministic solution converges to zero, and that if $a^2 - 4b < 0$, the exponents are complex numbers and so the solution is *underdamped*, i.e., has a cyclic component. It can be expected then that the same cyclic component will turn up if the orbit is perturbed by white noise, because that is what happens in the SDE (26).

From the properties (a), (b) and (c) in the section 6.4, it can be deduced that

(d) $C_{\frac{d^2X}{dt^2},Y} = +C''_{X,Y}$

(e) $C_{X,\frac{d^2Y}{dt^2}} = +C''_{X,Y}$

(f) $C_{\frac{d^2X}{dt^2},\frac{dY}{dt}} = -C'''_{X,Y}$

(g) $C_{\frac{dX}{dt},\frac{d^2Y}{dt^2}} = +C'''_{X,Y}$

(h) $C_{\frac{d^2X}{dt^2},\frac{d^2Y}{dt^2}} = +C''''_{X,Y}$

The proof is left as an exercise. Applying these properties with $Y = X$ to the linear second-order auto-correlative process defined by (26) gives

$$C''''_{X,X} - (a^2 - 4b)C''_{X,X} + b^2C_{X,X} = c^2\delta \tag{30}$$

where δ is the Dirac delta distribution. Taking Fourier transforms yields

$$\omega^4 S_{X,X} + (a^2 - 4b)\omega^2 S_{X,X} + b^2 S_{X,X} = c^2 \tag{31}$$

and so

$$S_{X,X}(\omega) = \frac{c^2}{\omega^4 + (a^2 - 4b)\omega^2 + b^2} \tag{32}$$

The inverse Fourier transform gives the auto-covariance, but I didn't manage to do that analytically. Once we have the spectral density, however, we can calculate its inverse Fourier transform by numerical integration, as was done in the figure below.

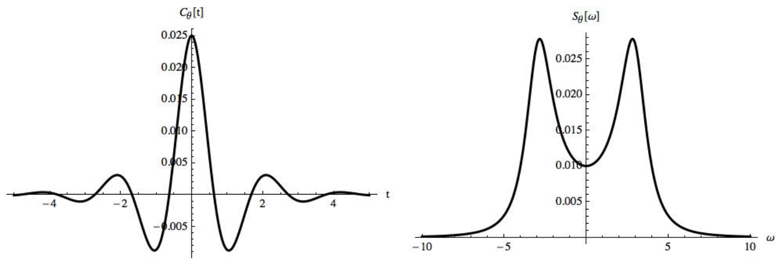

FIGURE 5. Auto-covariance and spectral density for the underdamped linear second-order auto-correlative process (26) with $a = 2$, $b = 10$ and $c = 1$.

The damped oscillations in the $C_{X,X}$ are the telltale sign of a so-called *phase-forgetting quasi cycle*. The peaks in the spectral density correspond to the frequency of the solution of the corresponding homogeneous ordinary differential equation (28) with the same values of a, b and c.

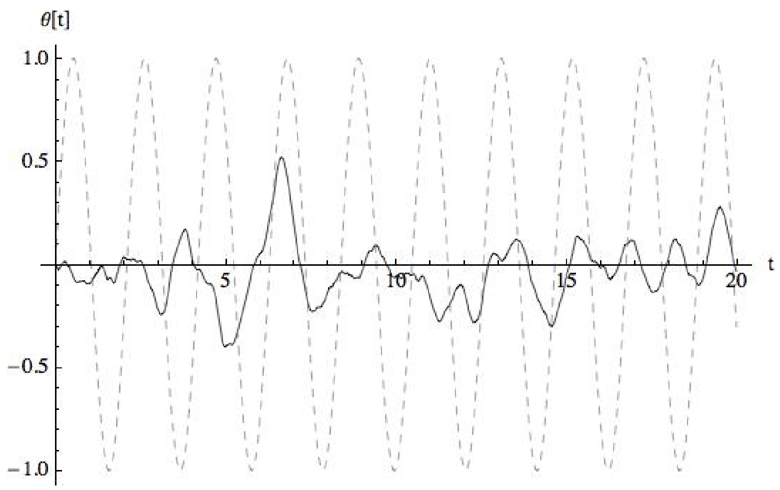

FIGURE 6. Sample path of the underdamped linear second-order auto-correlative process (26) with $a = 2$, $b = 10$ and $c = 1$. The dashed line is a sine wave with the same frequency that peaks in the plot of the spectral density. Notice the quasi-periodic character of the sample path.

6.6. **Integrated noise.** Every measurement takes time. No physical instrument can measure the instantaneous value of a signal. Instead it measures a (weighed) average of the signal over a given (possibly very short) period of time. The same is true for organisms: because of slow reaction times, individuals react to averages of temperature, moisture and the like. This is our motivation to look at the following problem: given the stochastic process $\{X(t)\}$ define

$$Y(t) := \int_0^\infty X(t-\tau)\varphi(\tau)d\tau \tag{33}$$

for some given probability distribution φ. How do we calculate the auto-covariance and spectral density of the process $\{Y(t)\}$ if those for $\{X(t)\}$ are given? We shall address this problem not in general, but only for the case when φ is the uniform distribution or the exponential distribution.

Uniform distribution:

Suppose that φ is the uniform distribution on the time interval $(0, \Delta t)$. Then

$$Y(t) := \frac{1}{\Delta t}\int_0^{\Delta t} X(t-\tau)d\tau \tag{34}$$

Differentiating with respect to time gives

$$\begin{aligned} \tfrac{d}{dt}Y(t) &= \tfrac{1}{\Delta t}\int_0^{\Delta t} \tfrac{d}{dt}X(t-\tau)d\tau \\ &= \tfrac{-1}{\Delta t}\int_0^{\Delta t} \tfrac{d}{d\tau}X(t-\tau)d\tau \\ &= \tfrac{1}{\Delta t}\Big(X(t) - X(t-\Delta t)\Big) \end{aligned} \tag{35}$$

Equating the auto-covariance function of the left and right side gives

$$-C_Y'' = \frac{1}{(\Delta t)^2}\Big(C_{X,X} - C_{X,X_{\Delta t}} - C_{X_{\Delta t},X} + C_{X_{\Delta t},X_{\Delta t}}\Big) \tag{36}$$

where $X_{\Delta t}(t) := X(t-\Delta t)$. One readily sees that

(i) $C_{X,X_{\Delta t}}(\tau) = \mathcal{E}\big\{X(t+\tau) - X(t-\Delta t)\big\} = C_X(\tau + \Delta t)$

(j) $C_{X_{\Delta t},X}(\tau) = \mathcal{E}\big\{X(t-\Delta t+\tau) - X(t)\big\} = C_X(\tau - \Delta t)$

(k) $C_{X_{\Delta t},X_{\Delta t}}(\tau) = \mathcal{E}\big\{X(t-\Delta t+\tau) - X(t-\Delta t)\big\} = C_X(\tau)$

Applying this to equation (36), we have

$$-C_Y''(\tau) = \frac{1}{(\Delta t)^2}\Big(2C_X - C_X(\tau+\Delta t) - C_X(\tau - \Delta t)\Big) \tag{37}$$

Taking Fourier transforms gives

$$\omega^2 S_Y(\omega) = \frac{1}{(\Delta t)^2}\Big(2 - e^{i\omega\Delta t} - e^{-i\omega\Delta t}\Big)S_X(\omega) \tag{38}$$

and so

$$S_Y(\omega) = \frac{2(1-\cos\omega\Delta t)}{(\omega\Delta t)^2}S_X(\omega) \tag{39}$$

Taking inverse Fourier transforms gives

$$C_Y(\tau) = \int_{-\infty}^{+\infty} \Phi(t)C_X(\tau - t)dt =: (\Phi * C_X)(\tau) \tag{40}$$

i.e., the convolution of Φ and C_X, where Φ is the inverse Fourier transform of $2(1-\cos\omega\Delta t)/(\omega\Delta t)^2$, which is

$$\Phi(\tau) := \begin{cases} \frac{1}{\Delta t^2}(\Delta t - |\tau|) & \text{if } |\tau| \leq \Delta t \\ 0 & \text{otherwise} \end{cases} \tag{41}$$

and which is immediately recognized as the auto-covariance function of the (scaled) Wiener increment $\{\Delta W(t)/\Delta t\}$ (see section 6.3).

Exponential distribution:

Suppose that φ is the exponential distribution with parameter λ. Then

$$Y(t) := \lambda \int_0^\infty e^{-\lambda\tau} X(t-\tau) d\tau \tag{42}$$

Differentiating with respect to time gives

$$\begin{aligned} \tfrac{d}{dt}Y(t) &= \lambda \textstyle\int_0^\infty e^{-\lambda\tau} \tfrac{d}{dt} X(t-\tau)d\tau \\ &= -\lambda \textstyle\int_0^\infty e^{-\lambda\tau} \tfrac{d}{d\tau} X(t-\tau)d\tau \\ &= -\lambda\big[e^{-\lambda\tau}X(t-\tau)\big]_0^\infty - \lambda^2 \textstyle\int_0^\infty e^{-\lambda\tau} X(t-\tau)d\tau \\ &= \lambda X(t) - \lambda Y(t) \end{aligned} \tag{43}$$

Taking the $-\lambda Y(t)$ to the left hand side gives

$$\frac{d}{dt}Y(t) + \lambda Y(t) = \lambda X(t) \tag{44}$$

It can immediately be seen that if $\{X(t)\}$ is the *Gaussian white noise*, then $\{Y(t)\}$ is the Ornstein-Uhlenbeck process from Section 6.4 with $a = b = \lambda$.

Using the properties (a), (b) and (c), we find

$$-C_Y'' + \lambda^2 C_Y = \lambda^2 C_X \tag{45}$$

and hence

$$\omega^2 S_Y + \lambda^2 S_Y = \lambda^2 S_X \tag{46}$$

and so

$$S_Y(\omega) = \frac{\lambda^2}{\omega^2+\lambda^2} S_X \tag{47}$$

Taking the inverse Fourier transform, we find

$$C_Y(\tau) = \int_{-\infty}^{+\infty} \Phi(t) C_X(\tau - t)dt =: (\Phi * C_X)(\tau) \tag{48}$$

i.e., the convolution of Φ and C_X, where Φ is the inverse Fourier transform of $\lambda^2/(\omega^2+\lambda^2$, which is

$$\Phi(\tau) := \frac{1}{2}\lambda e^{-\lambda|\tau|} \tag{49}$$

i.e., the auto-covariance function of the Ornstein-Uhlenbeck process from Section 6.4 with $a = b = \lambda$.

6.7. **Functions of noise.** Suppose $\{X(t)\}$ is a known stationary stochastic process with auto-covariance function $C_X(\tau)$ and spectral density $S_X(\omega)$, and for given function $h : \mathbb{R} \to \mathbb{R}$ let

$$Y(t) := h(X(t)) \tag{50}$$

What do the auto-covariance and spectral density of of the process $\{Y(t)\}$ look like? In all our applications we consider low amplitude noise, i.e., noise with a low variance. Assuming that the function h is at least twice differentiable, we can make the following approximations by second-order Taylor expansion of $h(X)$ about value $\bar{X}$:

$$\begin{aligned} \bar{Y} &= \mathcal{E}\big\{h(X(t))\big\} \\ &\approx h(\bar{X}) + \tfrac{1}{2}h''(\bar{X})C_X(0) \end{aligned} \tag{51}$$

and

$$\begin{aligned} \mathcal{E}\big\{Y(t+\tau)Y(t)\big\} &= \mathcal{E}\big\{h(X(t+\tau))h(X(t))\big\} \\ &\approx h(\bar{X})^2 + h(\bar{X})h''(\bar{X})C_X(0) + h'(\bar{X})^2 C_X(\tau) \end{aligned} \tag{52}$$

and hence

$$\begin{aligned} C_Y(\tau) &= \mathcal{E}\big\{Y(t+\tau)Y(t)\big\} - \bar{Y}^2 \\ &\approx h'(\bar{X})^2 C_X(\tau) \end{aligned} \tag{53}$$

and

$$S_Y(\omega) \approx h'(\bar{X})^2 S_X(\omega) \tag{54}$$

Birth rates and death rates are necessarily positive and may be log-normally distributed.

As an example, let $Y(t)$ be a stochastic birth rate given by

$$Y(t) := c\, e^{X(t)} \quad (c > 0) \tag{55}$$

where $\{X(t)\}$ is the stationary Ornstein-Uhlenbeck process generated by

$$\mathrm{d}X + aX\mathrm{d}t = b\mathrm{d}W \quad (a > 0) \tag{56}$$

Then,

$$X(t) \sim \mathcal{N}\left(0, \frac{b^2}{2a}\right) \tag{57}$$

$$C_X(\tau) = \frac{b^2}{2a} e^{-a|\tau|} \tag{58}$$

and

$$S_X(\tau) = \frac{b^2}{\omega^2 + a^2}\ . \tag{59}$$

Consequently,

$$\log Y(t) \sim \mathcal{N}\left(\log c, \frac{b^2}{2a}\right) \tag{60}$$

$$\bar{Y} \approx c + \frac{c}{2}C_X(0) = c\left(1 + \frac{b^2}{4a}\right) \tag{61}$$

$$C_Y(\tau) \approx c^2 C_X(\tau) = \frac{b^2c^2}{2a}e^{-a|\tau|} \tag{62}$$

and

$$S_Y(\omega) \approx c^2 S_X(\omega) = \frac{b^2c^2}{\omega^2 + a^2}\ . \tag{63}$$

Compare the above approximate values of the mean and variance of $Y(t)$ with their exact values

$$\bar{Y} = ce^{\frac{b^2}{4a}} = c\left(1 + \frac{b^2}{4a} + \dots\right) \tag{64}$$

and

$$C_Y(0) = c^2\left(e^{\frac{b^2}{2a}} - 1\right)e^{\frac{b^2}{2a}} = c^2\left(\frac{b^2}{2a} + \dots\right) \tag{65}$$

which can be calculated directly from the log-normal probability density or you can look them up in a table of probability distributions.