Populations Models: Part I

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UQ School of Maths and Physics

Mathematics Enrichment Seminars

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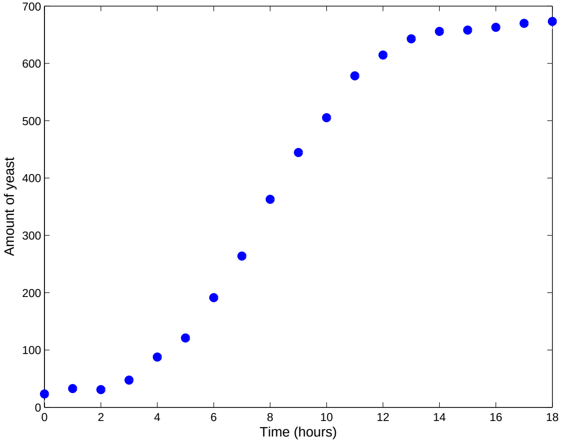
Growth of yeast



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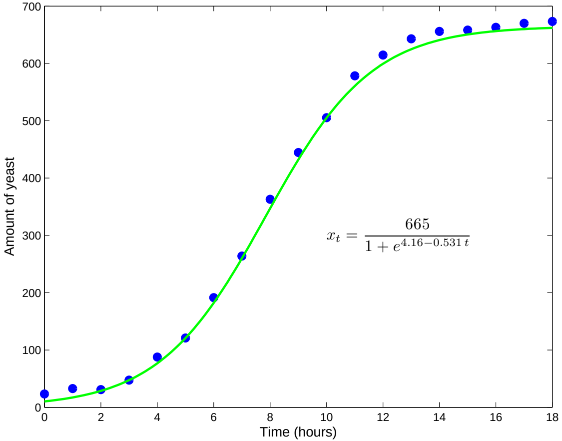

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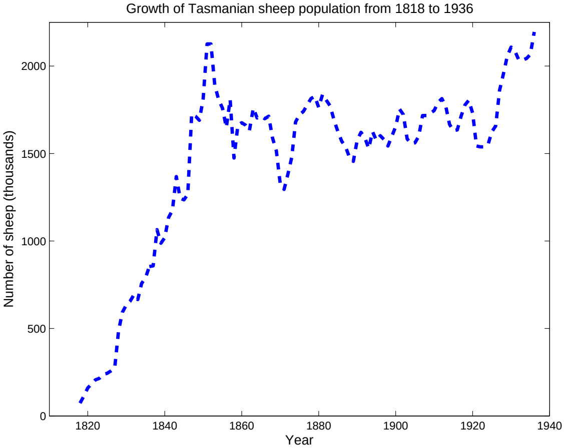

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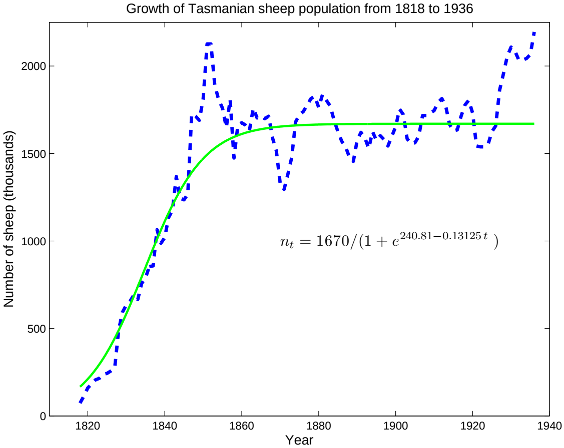

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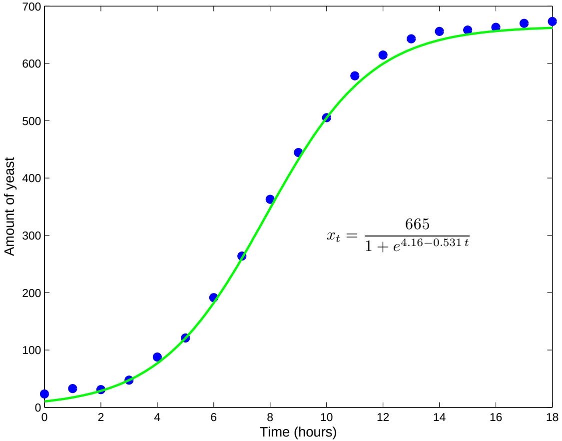

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A deterministic model

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The net growth rate per individual is a function of the population size n.

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This is the Verhulst model (or *logistic model*):

Verhulst, P.F. (1838) Notice sur la loi que la population suit dans son accroisement. *Corr. Math. et Phys.* X, 113–121.

The Verhulst model

Pierre Francois Verhulst (1804–1849, Brussels, Belgium)

Soit p la population : représentons par dp l'accroissement infiniment petit qu'elle reçoit pendant un temps infiniment court dt. Si la population croissait en progression géométrique, nous aurions l'équation $\frac{dp}{dt} = mp$. Mais comme la vitesse d'accroissement de la population est retardée par l'augmentation même du nombre des habitans, nous devrons retrancher de mp une fonction inconnue de p; de manière que la formule à intégrer deviendra

$$\frac{dp}{dt} = mp - \varphi(p).$$

L'hypothèse la plus simple que l'on puisse faire sur la forme de la fonction φ, est de supposer $\varphi(p) = np^2$. On trouve alors pour intégrale de l'équation ci-dessus

$$t = \frac{1}{m}\left[\log. p - \log.(m - np)\right] + \text{constante},$$

et il suffira de trois observations pour déterminer lés deux coefficiens constans m et n et la constante arbitraire.

The Verhulst model

En résolvant la dernière équation par rapport à p, il vient

$$p = \frac{mp' e^{mt}}{np' e^{mt} + m - np'} \quad . \quad . \quad . \quad . \quad . \quad (1)$$

en désignant par p' la population qui répond à $t = o$, et par e la base des logarithmes népériens. Si l'on fait $t = \infty$, on voit que la valeur de p correspondante est $P = \frac{m}{n}$. Telle est donc *la limite supérieure de la population.*

Au lieu de supposer $\varphi p = np^2$, on peut prendre $\varphi p = np^\alpha$, α étant quelconque, ou $\varphi p = n \log. p$. Toutes ces hypothèses satisfont également bien aux faits observés ; mais elles donnent des valeurs très-différentes pour la limite supérieure de la population.

J'ai supposé successivement

$$\varphi p = np^2,\ \varphi p = np^3,\ \varphi p = np^4,\ \varphi p = n \log. p;$$

et les différences entre les populations calculées et celles que fournit l'observation ont été sensiblement les mêmes.

ACEMS

The Verhulst model

N° 1.

Tableau des progrès de la population de la France depuis 1817 *jusqu'à* 1831, *d'après l'Annuaire pour* 1834.

ANNÉES.	D'APRÈS L'ÉTAT CIVIL.	D'APRÈS LA FORMULE.	ERREUR proportion^le.	Logarithmes de la population calculée.
1817	29,981,336 195,902	29,981,336 208,281	0,0000	7,4768490
1818	30,177,238 161,948	30,189,500 204,500	+0,0004	7,4798565
1819	30,339,186 199,863	30,394,000 200,500	+0,0018	7,4827875
1820	30,539,049 188,227	30,594,500 197,300	+0,0018	7,4856461
1821	30,727,276 212,144	30,791,800 192,700	+0,0021	7,4884310
1822	30,939,420 198,634	30,984,500 189,500	+0,0014	7,4911453
1823	31,138,054 221,286	31,174,000 185,223	+0,0012	7,4937907
1824	31,359,340 220,546	31,359,340 182,777	0,0000	7,4963719
1825	31,579,886 175,974	31,542,000 178,000	—0,0012	7,4988859
1826	31,755,860 157,533	31,720,000 175,000	—0,0011	7,5013366
1827	31,913,393 189,071	31,895,000 172,000	—0,0005	7,5037257
1828	32,102,464 139,402	32,067,000 168,000	—0,0011	7,5060547
1829	32,241,866 161,074	32,235,000 164,500	—0,0002	7,5083251
1830	32,402,940 157,994	32,399,500 161,434	0,0000	7,5105385
1831 1^r janv.	32,560,934 (Chiffre du recens^t.)	32,560,934	0,0000	7,5126965

"We will give the name *logistic* to the curve" - Verhulst 1845

Cette équation étant intégrée donne, en observant que $t=0$ répond à $p=b$,

$$t = \frac{1}{m} \log. \left[\frac{p(m - nb)}{b(m - np)} \right] \quad \ldots\ldots\ldots \quad (4)$$

Nous donnerons le nom de *logistique* à la courbe (*voyez la figure*)

tenu compte de la propriété dont jouissent les denrées alimentaires, de se multiplier dans une progression plus rapide que l'espèce humaine, lorsque le sol est nouvellement cultivé. Mais cet âge d'or de la société n'existe plus depuis longtemps pour les nations européennes. Quant aux ressources qu'un grand peuple peut tirer du commerce étranger pour se procurer des subsistances, il nous suffira de rappeler que, d'après les calculs de M. Moreau de Jonnès, la récolte de la France, en blé seulement, est de 70 millions d'hectolitres, et que pour transporter une pareille masse, il faudrait 88,000 navires de cent tonneaux ! Qu'on juge alors de la quantité des autres denrées alimentaires. Lors même qu'une partie considérable de la population française pourrait être nourrie de blés étrangers, jamais un gouvernement sage ne consentira à faire dépendre l'existence de millions de citoyens du bon vouloir des souverains étrangers.

Verhulst, P.F. (1845) Recherches mathématiques sur la loi d'accroissement de la population. *Nouveaux mémoires de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles*

The Verhulst model

An alternative formulation has r being the growth rate with unlimited resources and K being the "natural" population size (the *carrying capacity*). We put $f(n) = r(1 - n/K)$ giving

$$\frac{dn}{dt} = rn(1 - n/K),$$

which is the original model with $s = r/K$.

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This formulation is due to Raymond Pearl:

Pearl, R. and Reed, L. (1920) On the rate of growth of population of the United States since 1790 and its mathematical representation. *Proc. Nat. Academy Sci.* 6, 275–288.

Pearl, R. (1925) *The biology of population growth*, Alfred A. Knopf, New York.

Pearl, R. (1927) The growth of populations. *Quart. Rev. Biol.* 2, 532–548.

Population growth in USA

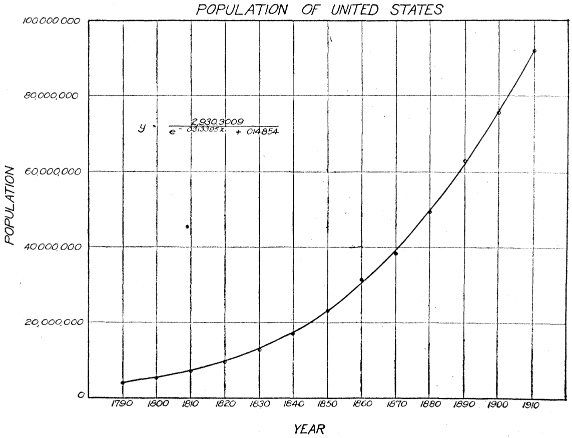

FIG. 3

Showing result of fitting equation (xviii) to population data.

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Verhulst-Pearl model

Raymond Pearl (1879–1940, Farmington, N.H., USA)

Pearl was a “social drinker”

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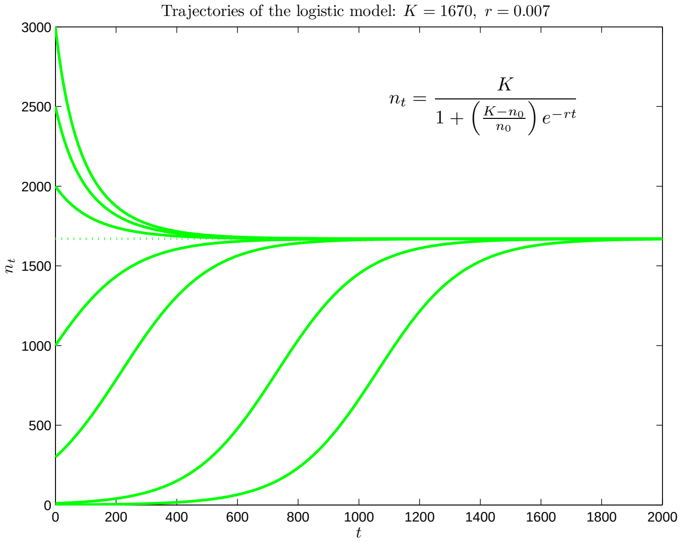
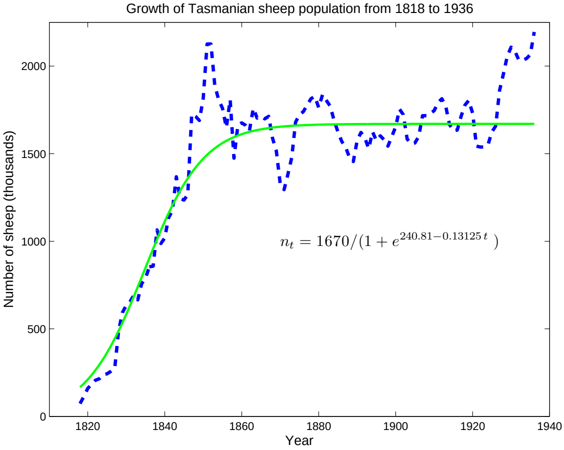
In 1926, his book, Alcohol and Longevity, demonstrated that drinking alcohol in moderation is associated with greater longevity than either abstaining or drinking heavily.

Pearl, R. (1926) *Alcohol and Longevity*, Alfred A. Knopf, New York.


Trajectories of the logistic model: $K = 1670,\ r = 0.007$
$$n_t = \frac{K}{1 + \left(\frac{K-n_0}{n_0}\right)e^{-rt}}$$
3000
2500
2000
1500
1000
500
0
n_t
0
200
400
600
800
1000
1200
1400
1600
1800
2000
t

Sheep in Tasmania



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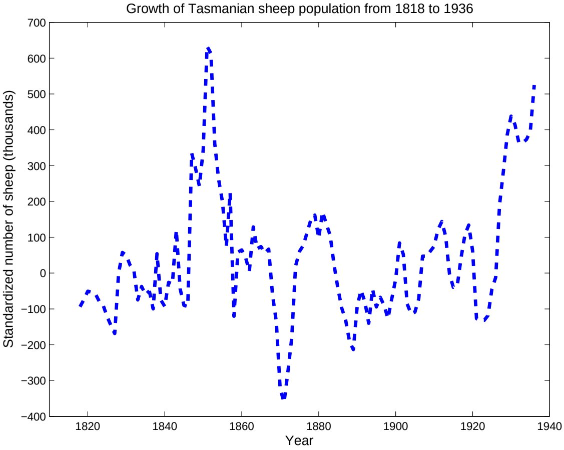

(With the deterministic trajectory subtracted)

A stochastic model

We really need to account for the variation observed.

A common approach to stochastic modelling in Applied Mathematics can be summarised as follows:

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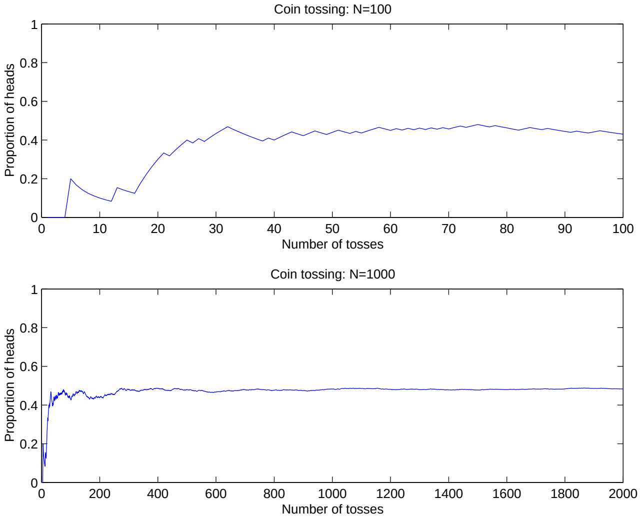
Zen Maxim (for survival in a modern university): Before you criticize someone, you should walk a mile in their shoes. That way, when you criticize them, you'll be a mile away and you'll have their shoes.

Coin tossing (fair coin)



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In fact, the *Central Limit Theorem*, as applied to coin tossing (de Moivre ($\simeq$1733)), shows that, as $t \to \infty$,

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So, it would not be completely unreasonable for us to write

$$p_t = \frac{1}{2} + \frac{1}{2\sqrt{t}} Z.$$

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In our case,

$$n_t = \frac{K}{1 + \left(\frac{K - n_0}{n_0}\right) e^{-rt}} + \text{something random}$$

or (much better)

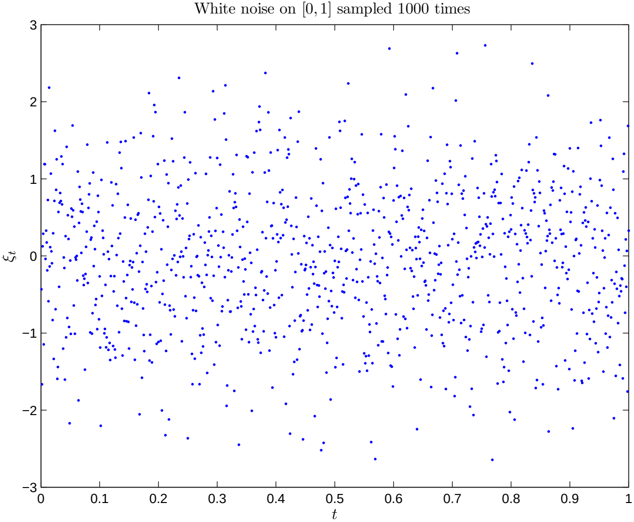
$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right) + \sigma \times \text{noise}.$$

Noise?

The usual model for "noise" is *white noise* (or *pure Gaussian noise*).

Imagine a random process $(\xi_t,\ t \geq 0)$ with $\xi_t \sim N(0,1)$ for all t and $\xi_{t_1}, \ldots, \xi_{t_n}$ *independent* for all finite sequences of times $t_1, \ldots, t_n$.

White noise

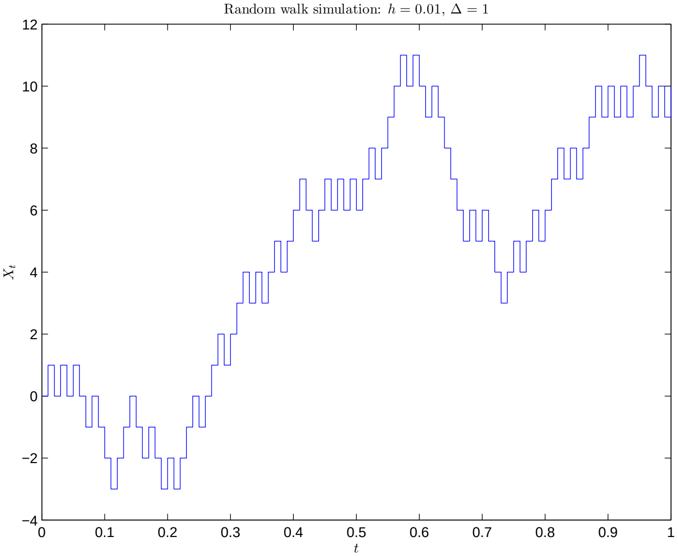

White noise on $[0, 1]$ sampled 1000 times
ξ_t
t
3
2
1
0
−1
−2
−3
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

Brownian motion

The white noise process $(\xi_t,\ t \geq 0)$ is loosely defined as the derivative of *standard Brownian motion* $(B_t,\ t \geq 0)$.

Brownian motion (or Wiener process) can be constructed by way of a random walk. A particle starts at 0 and takes small steps of size $+\Delta$ or $-\Delta$ with equal probability $p = 1/2$ after successive time steps of size h.

Symmetric random walk: $\Delta = 1$



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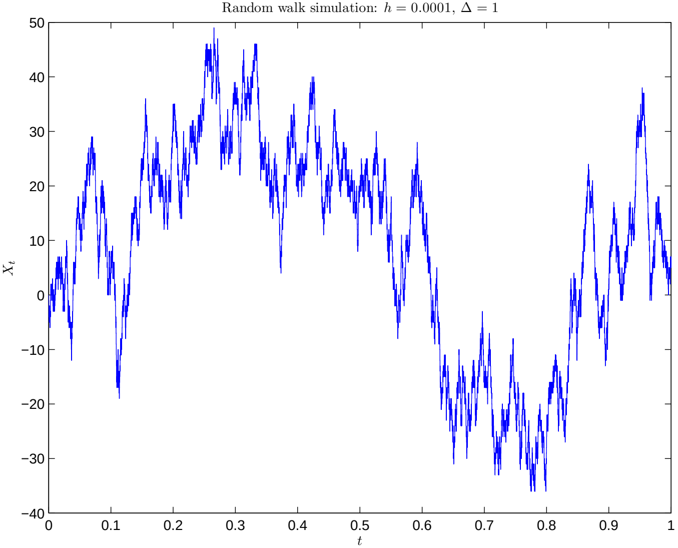

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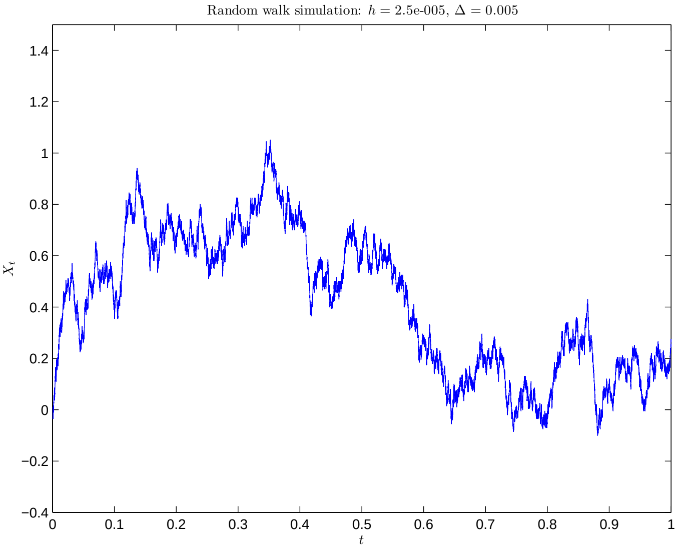

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This construction permits us to write $dB_t = \xi_t \sqrt{dt}$, with the interpretation that a change in B_t in time dt is a Gaussian random variable with $\mathbb{E}(dB_t) = 0$, $\mathrm{Var}(dB_t) = dt$ and $\mathrm{Cov}(dB_t, dB_s) = 0$ $(s \neq t)$.

[Recall that $\xi_t \sim N(0,1)$ for all t and $\xi_{t_1}, \ldots, \xi_{t_n}$ *independent* for all finite sequences of times $t_1, \ldots, t_n$.]

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General Brownian motion $(W_t,\ t \geq 0)$, with drift μ and variance σ^2, can be constructed in the same way but with $\Delta \sim \sigma\sqrt{h}$ and $p = \frac{1}{2}\left(1 + (\mu/\sigma)\sqrt{h}\right)$, and we may write

$$dW_t = \mu\, dt + \sigma\, dB_t,$$

with the interpretation that a change in W_t in time dt is a Gaussian random variable with $\mathbb{E}(dW_t) = \mu dt$, $\mathrm{Var}(dW_t) = \sigma^2 dt$ and $\mathrm{Cov}(dW_t, dW_s) = 0$.

Brownian motion

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It does not require an enormous leap of faith for us now to write down, and properly interpret, the SDE

$$dn_t = rn_t\,(1 - n_t/K)\,dt + \sigma dB_t$$

as a model for growth.

Adding noise

The idea (indeed the very idea of an SDE) can be traced back to Paul Langevin's 1908 paper "On the theory of Brownian Motion":

Langevin, P. (1908) Sur la théorie du mouvement brownien. *Comptes Rendus* 146, 530–533.

He derived a "dynamic theory" of Brownian Motion three years after Einstein's ground breaking paper on Brownian Motion:

Einstein, A. (1905) On the movement of small particles suspended in stationary liquids required by the molecular-kinetic theory of heat. *Ann. Phys.* 17, 549–560. [English translation by Anna Beck in *The Collected Papers of Albert Einstein*, Princeton University Press, Princeton, USA, 1989, Vol. 2, pp. 123–134.]

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In modern terminology, Langevin described the Brownian particle's velocity as an *Ornstein-Uhlenbeck (OU) process* and its position as the time integral of its velocity, while Einstein described its position as a Wiener process.

The *Langevin equation* (for a particle of unit mass) is

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This is Newton's law ($-\mu v = \text{Force} = m\dot{v}$) *plus* noise. The solution to this SDE is the OU process.

Paul Langevin (1872 – 1946, Paris, France)

Langevin

Einstein said of Langevin

"... It seems to me certain that he would have developed the special theory of relativity if that had not been done elsewhere, for he had clearly recognized the essential points."

Langevin was a dark horse

In 1910 he had an affair with *Marie Curie*.

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The person on the right is Langevin's PhD supervisor *Pierre Curie*.

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But, from Langevin's equation we have that

$$e^{\mu t} dv_t = -\mu e^{\mu t} v_t \, dt + \sigma e^{\mu t} dB_t,$$

and hence that $dy_t = \sigma e^{\mu t} dB_t$.

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We can deduce much from this. For example, v_t is a Gaussian process with $\mathbb{E}(v_t) = v_0 e^{-\mu t}$ and $\mathrm{Var}(v_t) = \frac{\sigma^2}{2\mu}(1 - e^{-2\mu t})$, and

$$\mathrm{Cov}(v_t, v_{t+s}) = \mathrm{Var}(v_t) e^{-\mu|s|}.$$

Where were we?

We had just added noise to our logistic model:

$$dn_t = rn_t \left(1 - \frac{n_t}{K}\right) dt + \sigma \, dB_t.$$

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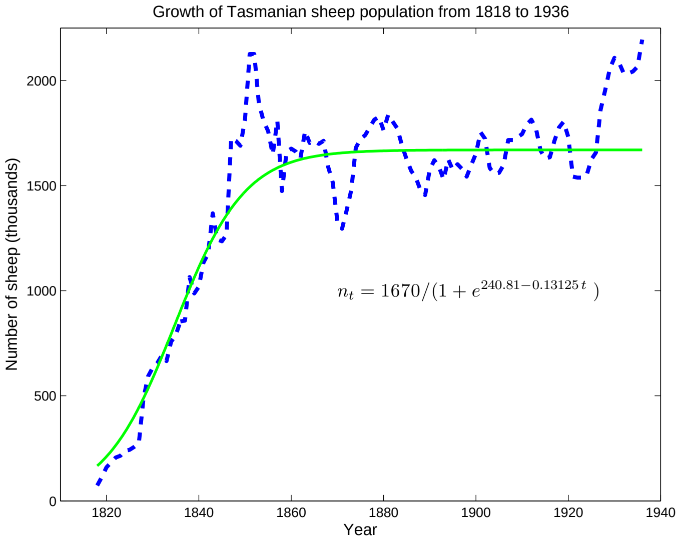
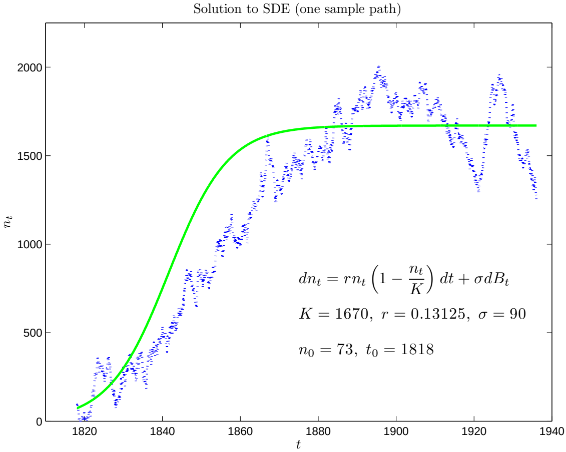
In Matlab ...

```
n = n + r*n*(1-n/K)*h + sigma*sqrt(h)*randn;
```

Sheep in Tasmania

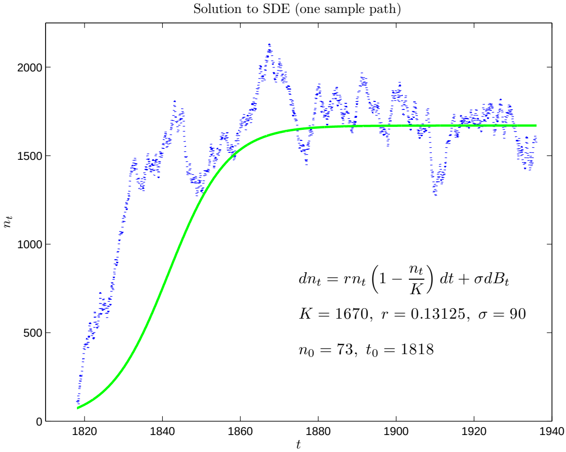


Solution to SDE (Run 1)



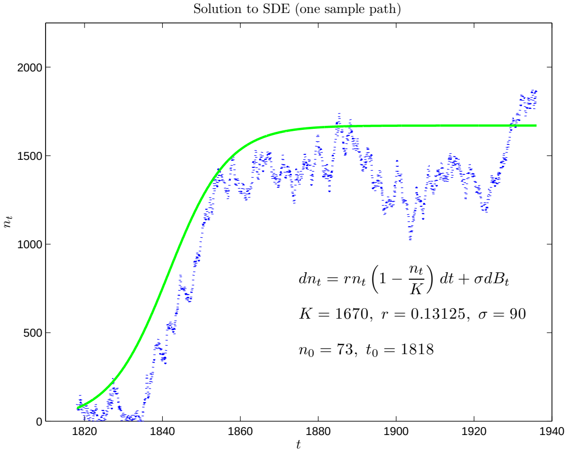
(Solution to the deterministic model is in green)

Solution to SDE (Run 2)



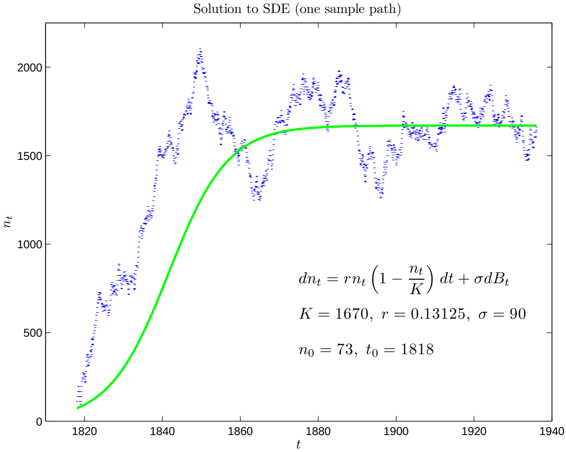
(Solution to the deterministic model is in green)

Solution to SDE (Run 3)



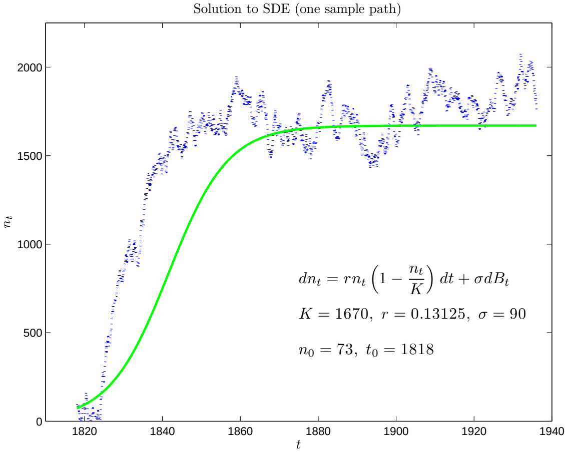
(Solution to the deterministic model is in green)

Solution to SDE (Run 4)



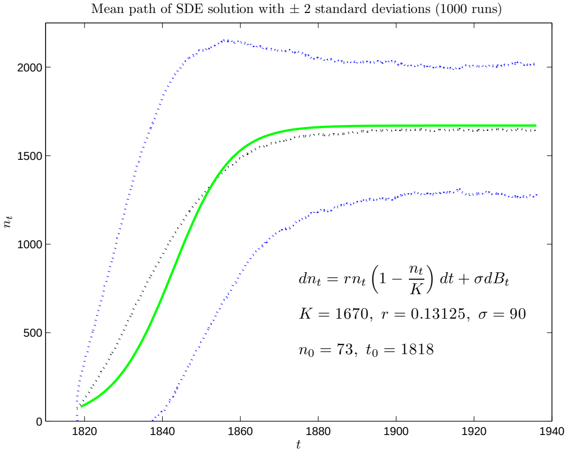
(Solution to the deterministic model is in green)

Solution to SDE (Run 5)



(Solution to the deterministic model is in green)

Solution to SDE



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Logistic model with noise

A significant problem with this approach (deterministic dynamics plus noise) is that variation is *not*, but *should be*, an integral component of the dynamics.

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Arguably a better approach is to use a continuous-time Markov chain to model n_t.

This will be dealt with in Part II or, if you prefer, STAT3004 "Probability Models & Stochastic Processes".