From rabbits in Canberra to convergence in $D[0, t]$: Part I

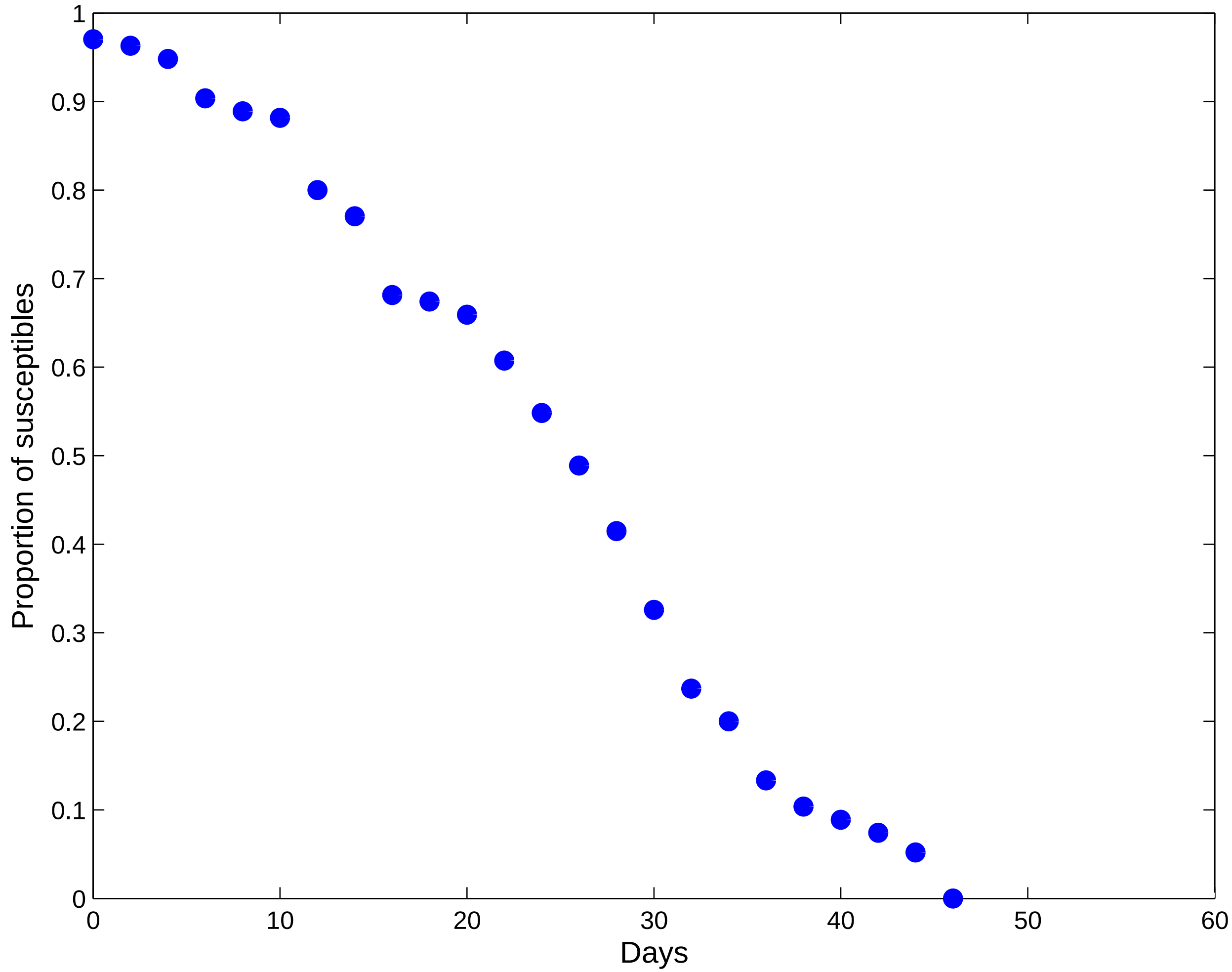
Phil Pollett

Department of Mathematics and MASCOS

University of Queensland

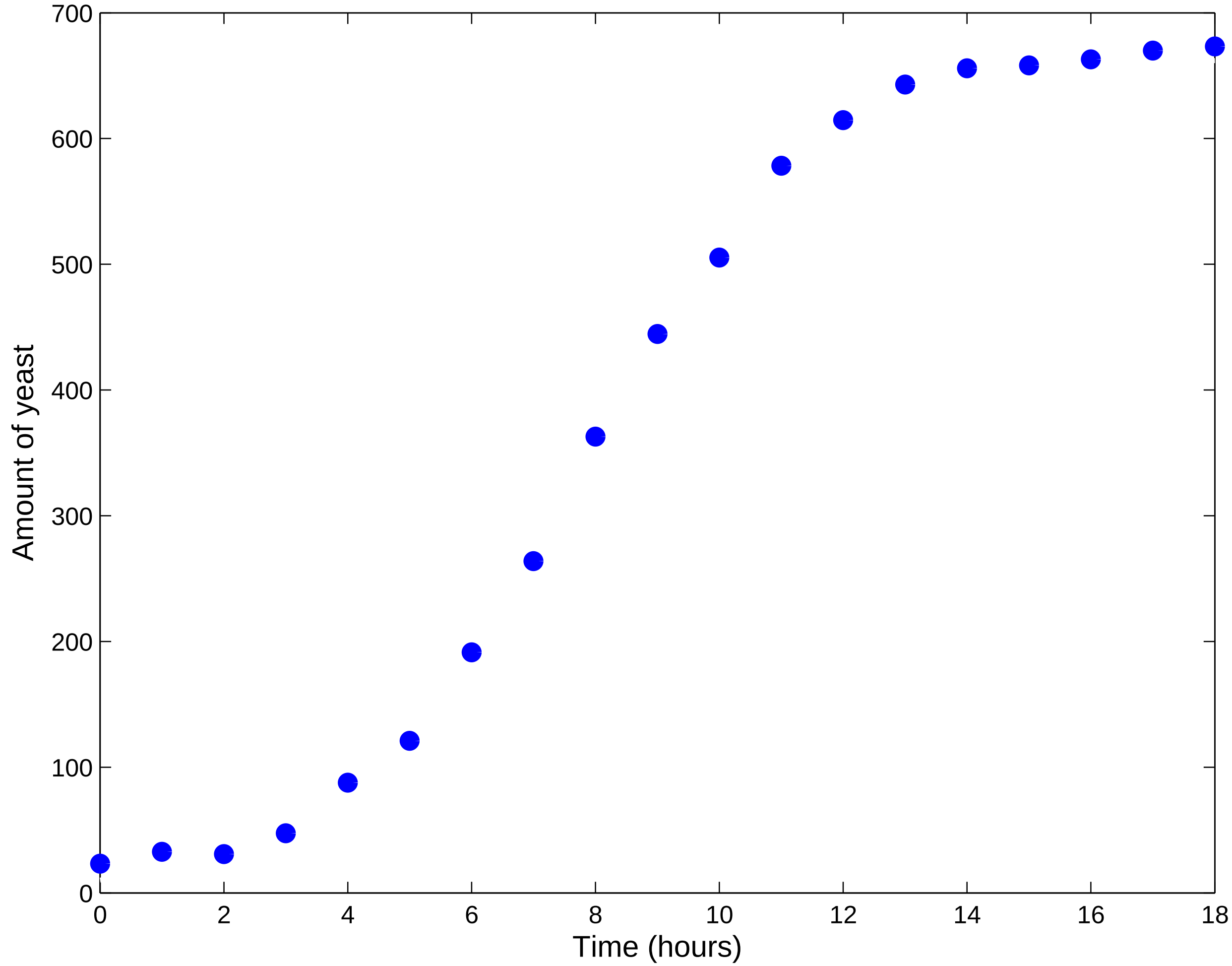
AUSTRALIAN RESEARCH COUNCIL
Centre of Excellence for Mathematics
and Statistics of Complex Systems

Rabbits in Canberra



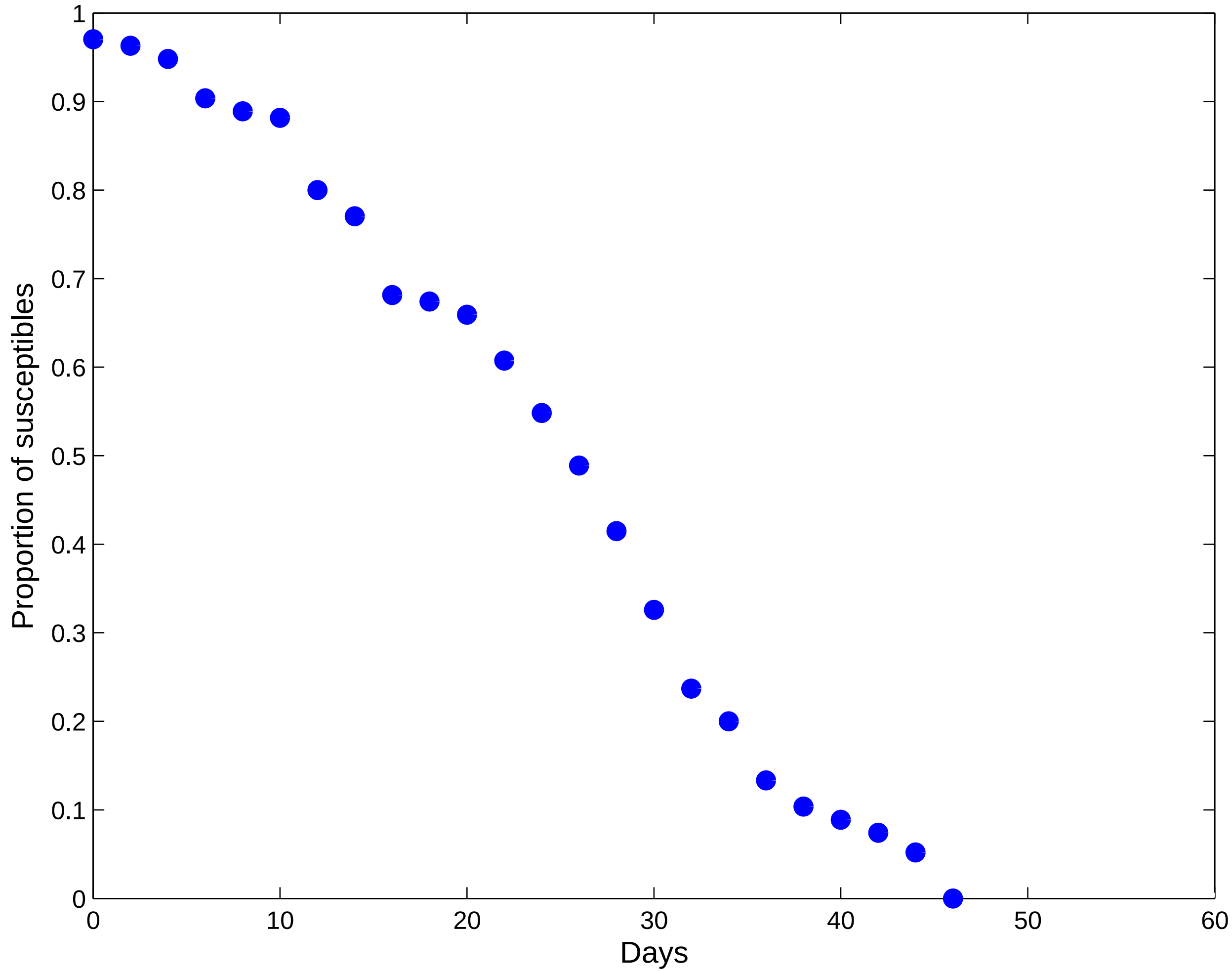
Williams, R.T., Fullagar, P.J., Kogon, C. and Davey, C. (1973) Observations on a naturally occurring winter epizootic of myxomatosis at Canberra, Australia, in the presence of Rabbit fleas (spilopsyllus cuniculi dale) and virulent myxoma virus, J. Appl. Ecol. 10, 417–427.

Growth of yeast



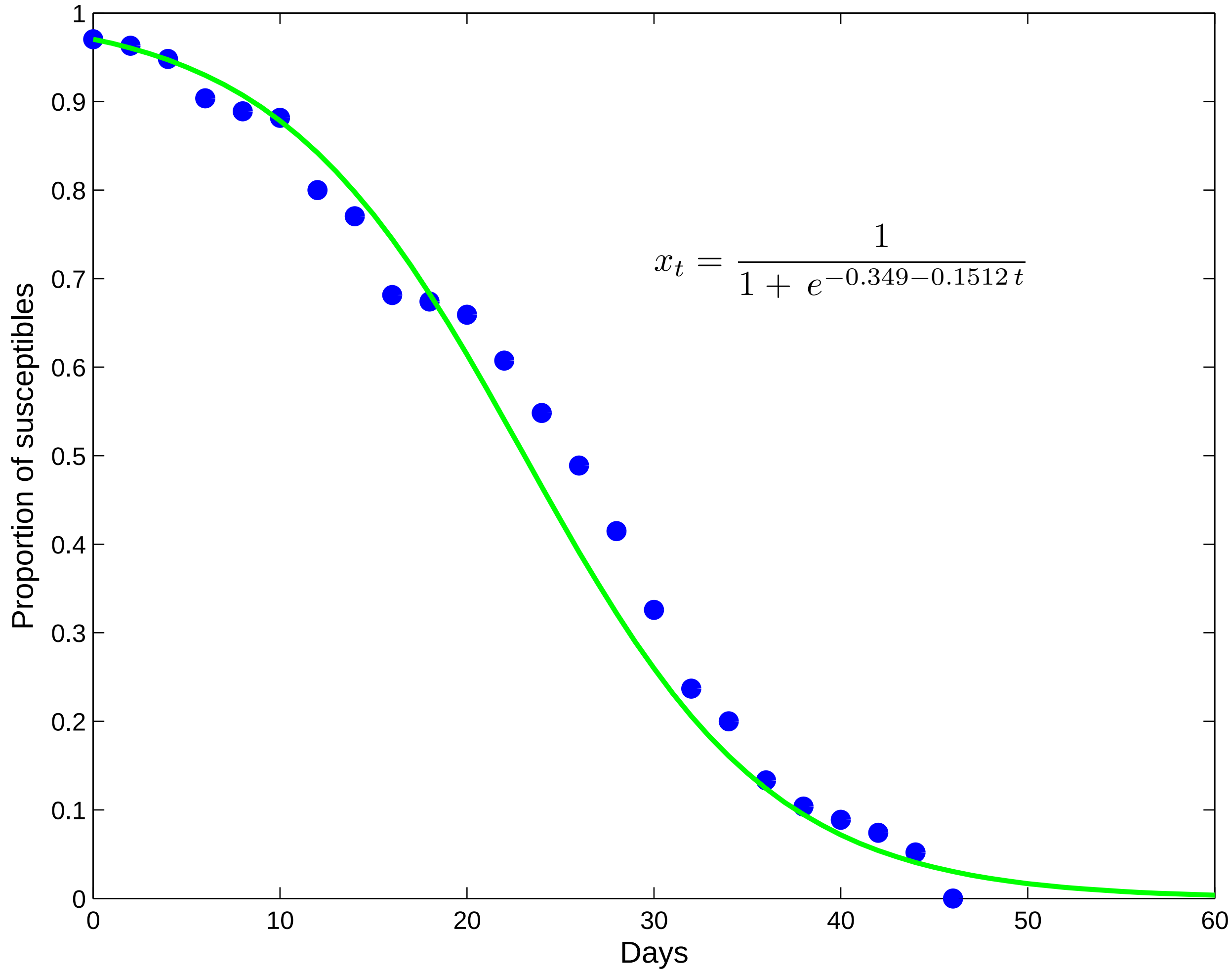
Carlson, T. (1913) Uber Geschwindigkeit und Grosse der Hefevermehrung in Wurze. Biochemische Zeitschrift 57, 313–334.

Rabbits in Canberra



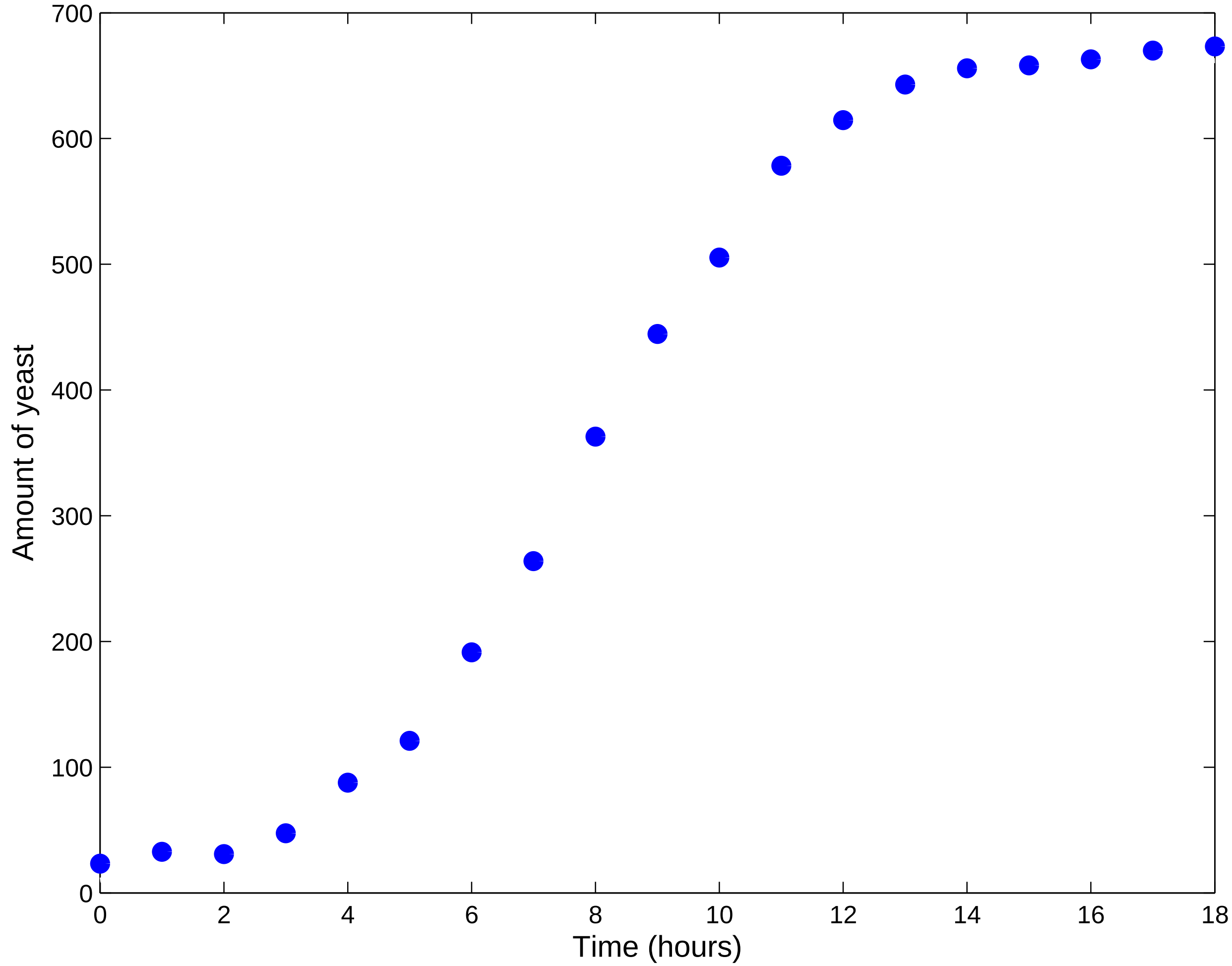
Williams, R.T., Fullagar, P.J., Kogon, C. and Davey, C. (1973) Observations on a naturally occurring winter epizootic of myxomatosis at Canberra, Australia, in the presence of Rabbit fleas (spilopsyllus cuniculi dale) and virulent myxoma virus, J. Appl. Ecol. 10, 417–427.

Rabbits in Canberra



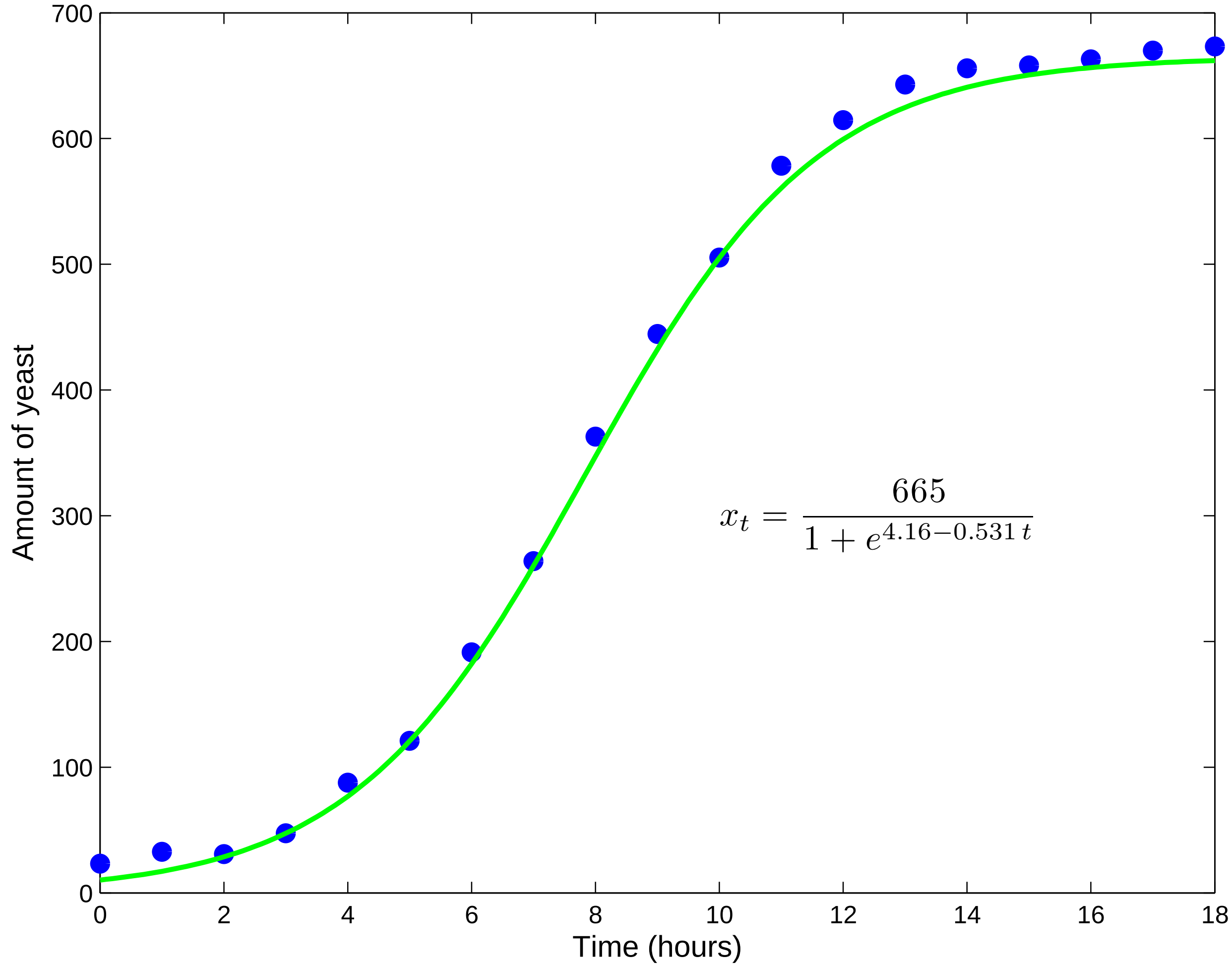
Williams, R.T., Fullagar, P.J., Kogon, C. and Davey, C. (1973) Observations on a naturally occurring winter epizootic of myxomatosis at Canberra, Australia, in the presence of Rabbit fleas (spilopsyllus cuniculi dale) and virulent myxoma virus, J. Appl. Ecol. 10, 417–427.

Growth of yeast



Carlson, T. (1913) Uber Geschwindigkeit und Grosse der Hefevermehrung in Wurze. Biochemische Zeitschrift 57, 313–334.

Growth of yeast



Carlson, T. (1913) Uber Geschwindigkeit und Grosse der Hefevermehrung in Wurze. Biochemische Zeitschrift 57, 313–334.

Population growth in USA

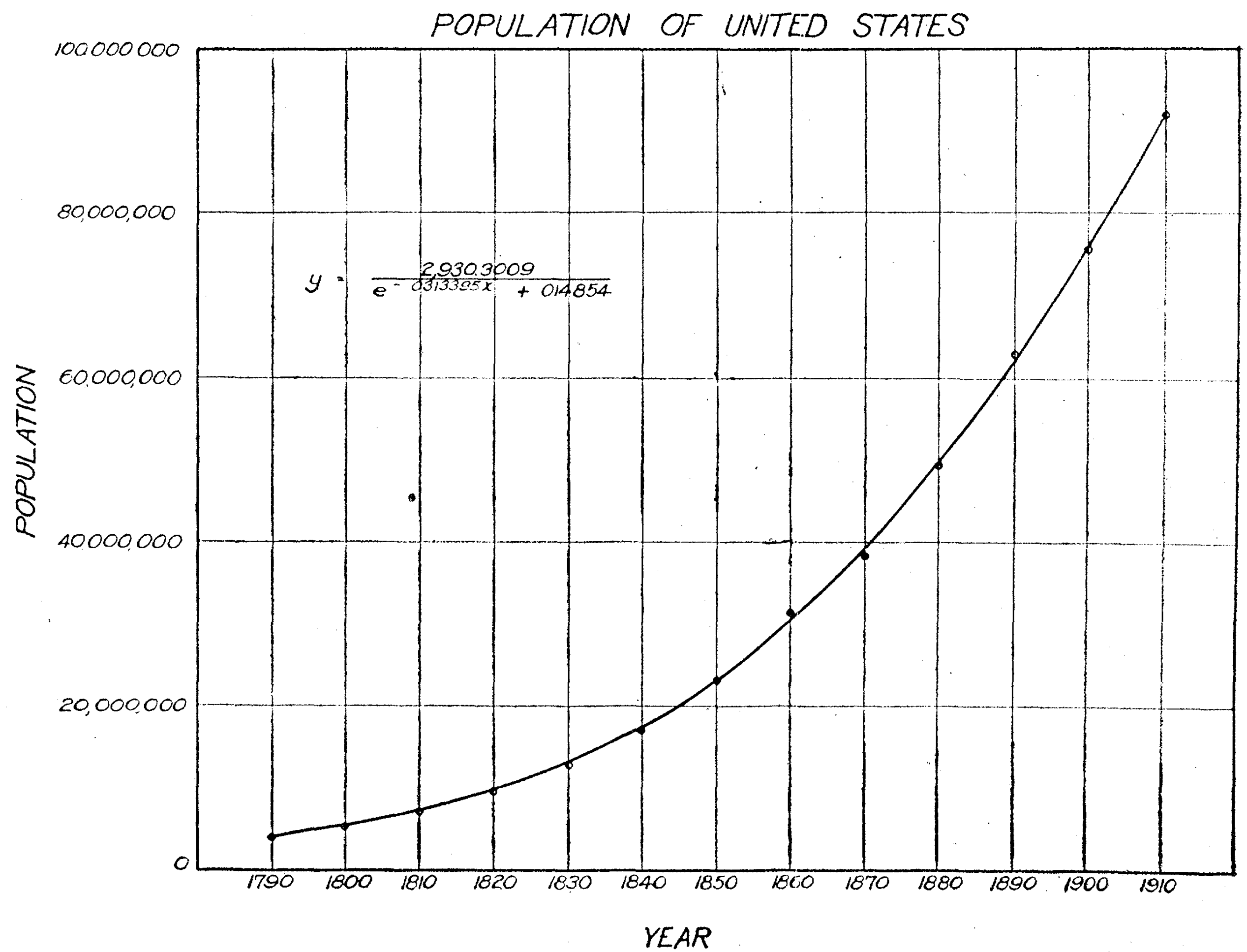
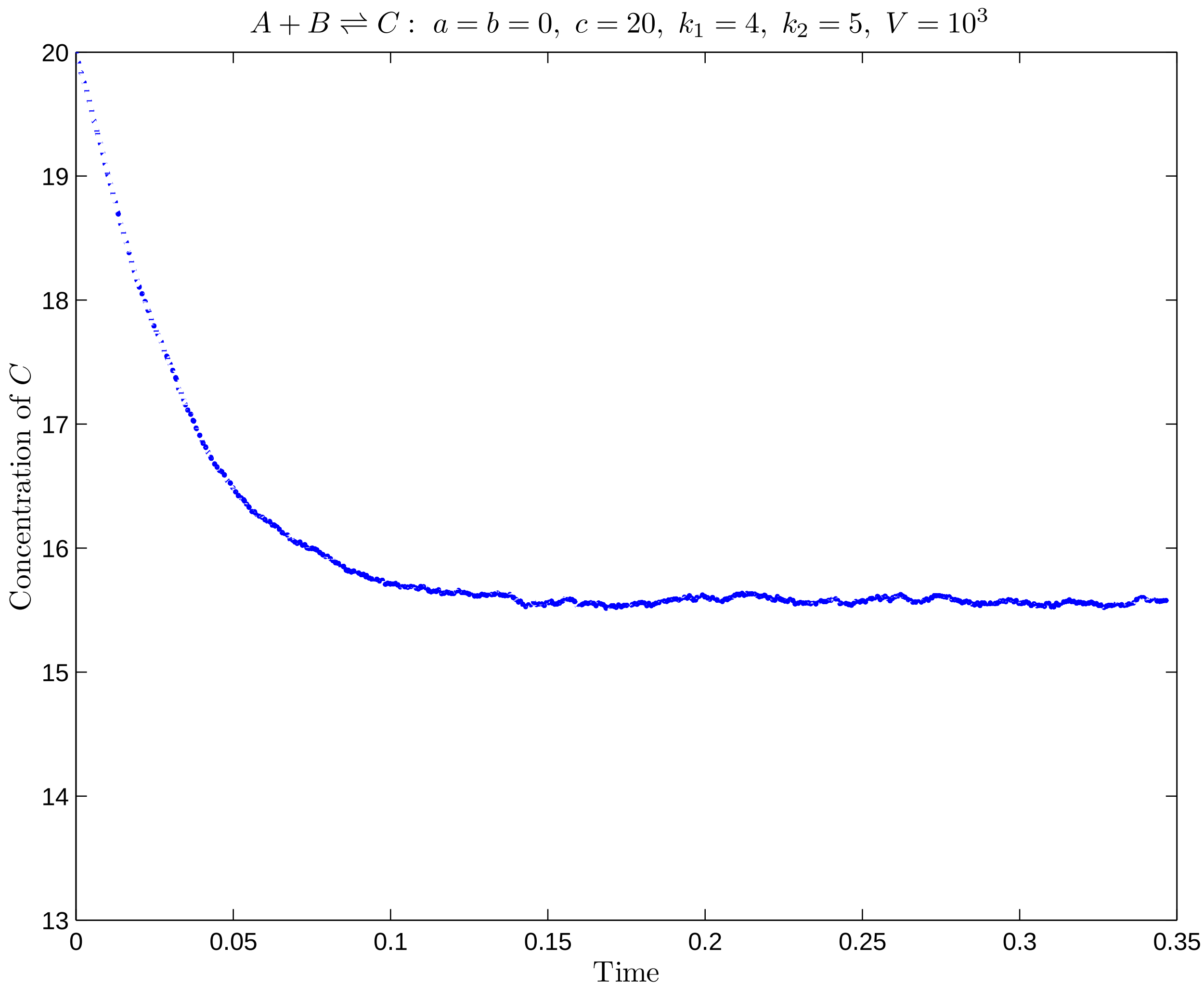


FIG. 3

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

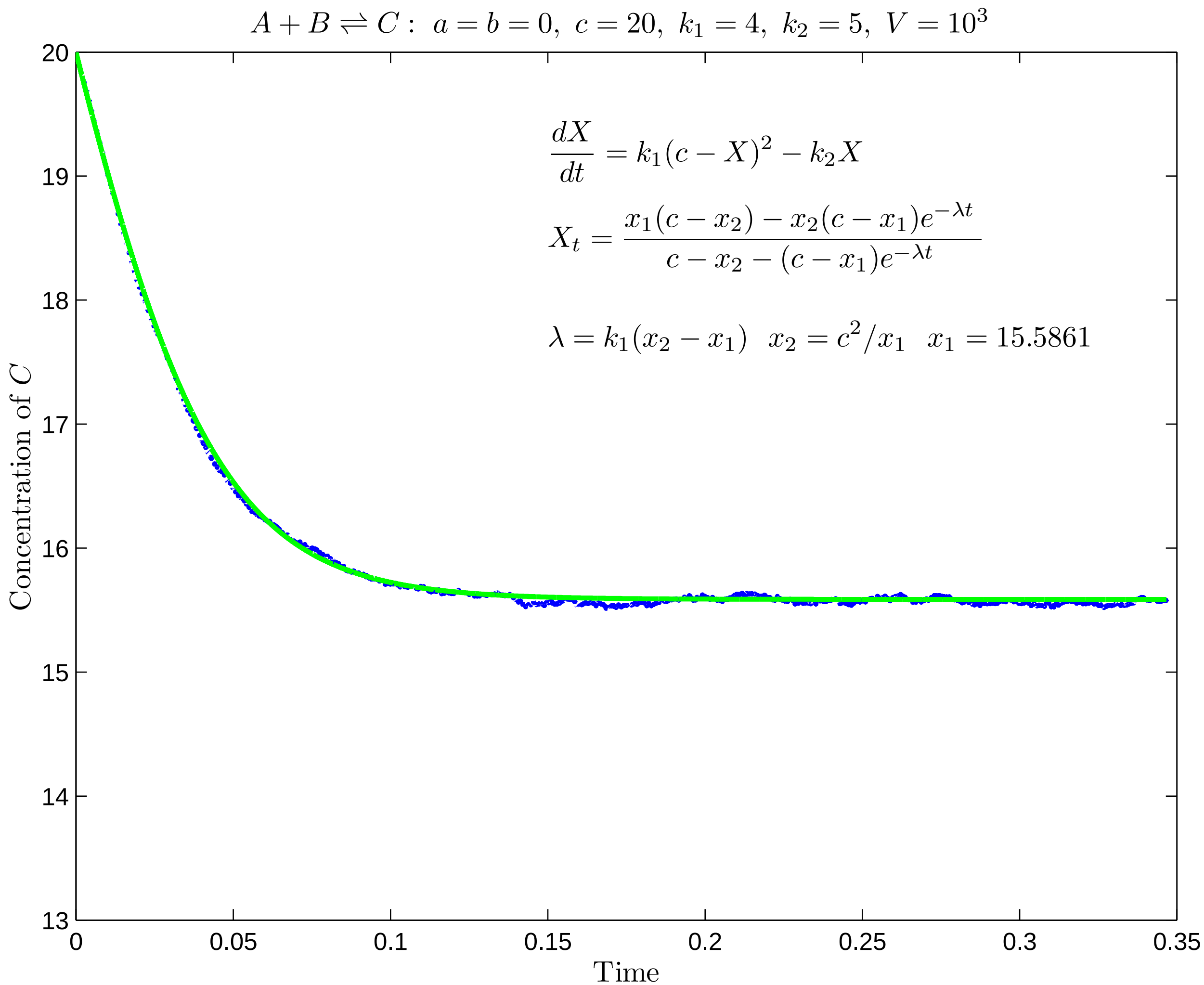
Pearl, R. and Reed, L. (1920) On the rate of growth of population of the United States since 1790 and its mathematical representation, Proc. Nat. Academy Sci. 6, 275–288.

A precipitation reaction



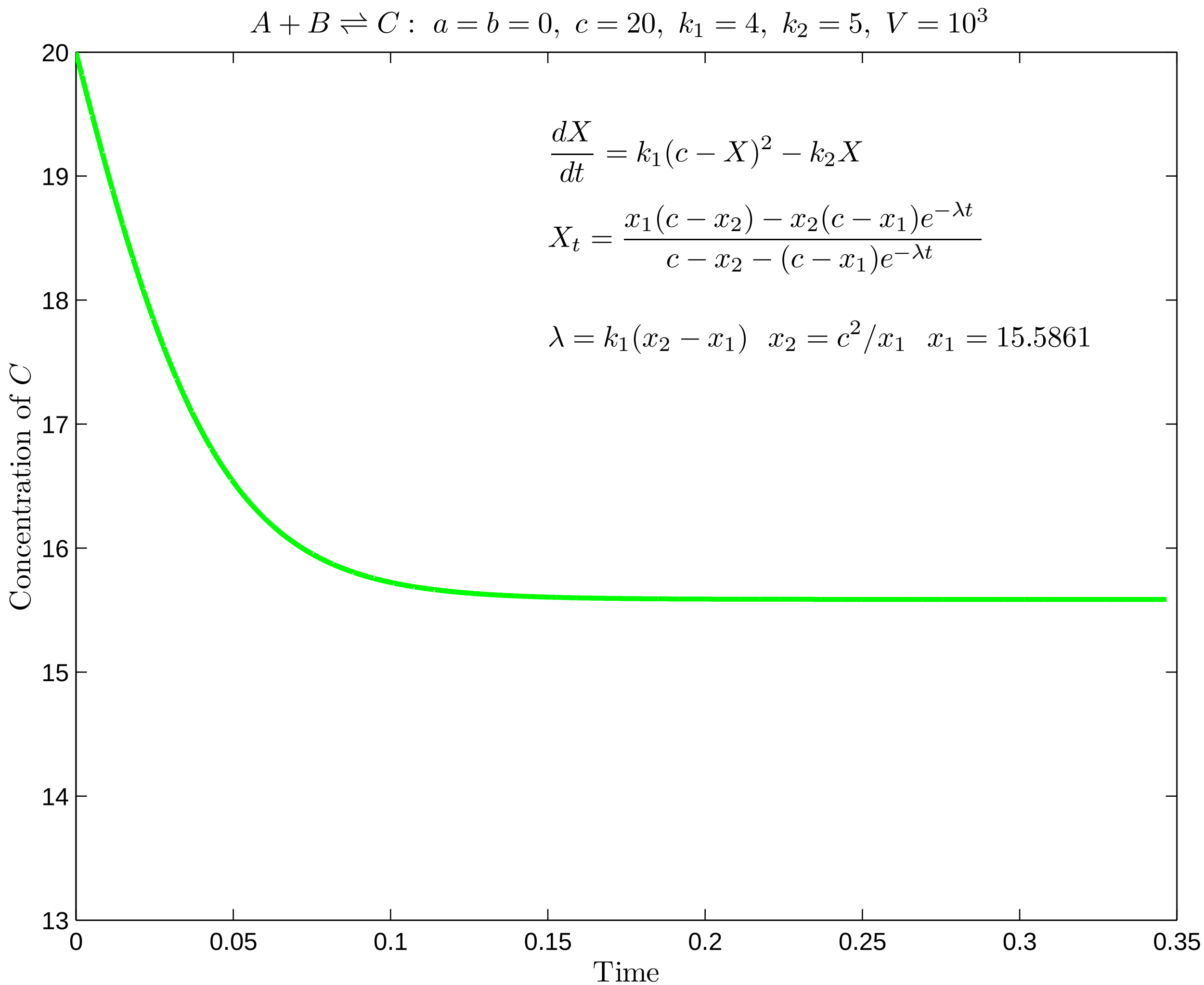
$Na^+ + Cl^- \rightleftharpoons NaCl$

A precipitation reaction



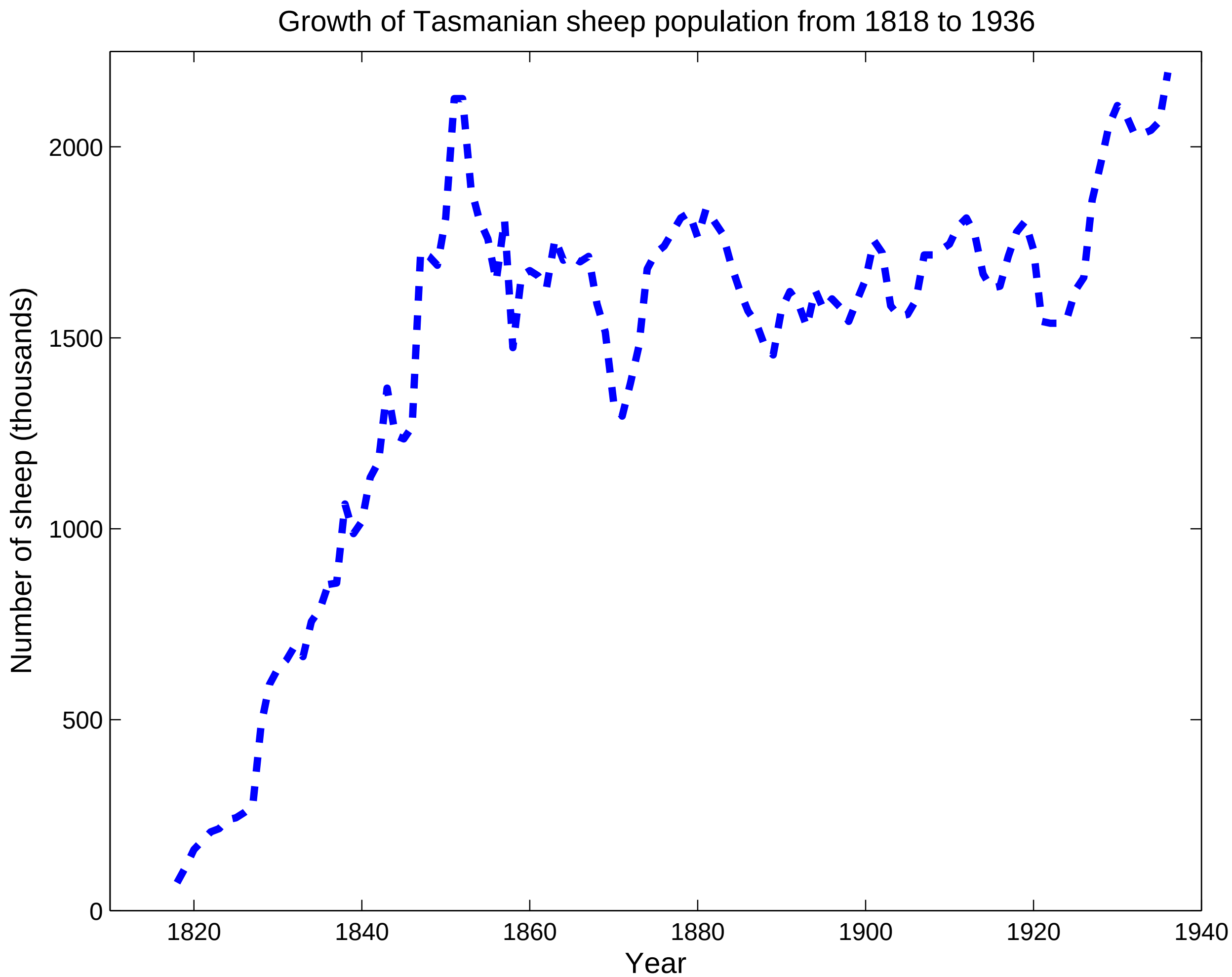
$\mathrm{Na}^+ + \mathrm{Cl}^- \rightleftharpoons \mathrm{NaCl}$

A precipitation reaction



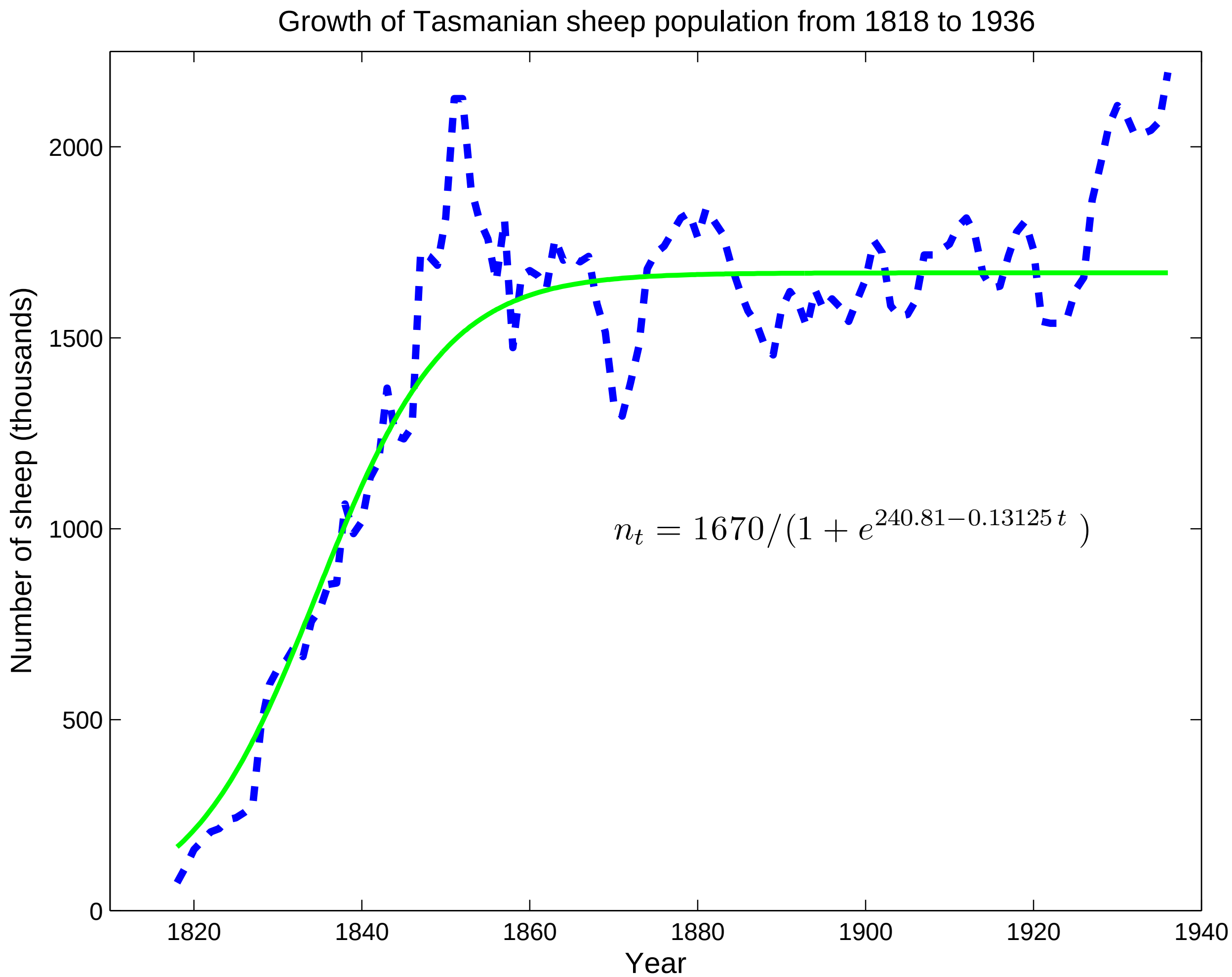
$Na^+ + Cl^- \rightleftharpoons NaCl$

Sheep in Tasmania



Davidson, J. (1938) On the growth of the sheep population in Tasmania, Trans. Roy. Soc. Sth. Austral. 62, 342–346.

Sheep in Tasmania



Davidson, J. (1938) On the growth of the sheep population in Tasmania, Trans. Roy. Soc. Sth. Austral. 62, 342–346.

A deterministic model

$$\frac{dn}{dt} = nf(n).$$

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

We want $f(n)$ to be positive for small n and negative for large n.

A deterministic model

$$\frac{dn}{dt} = nf(n).$$

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

We want $f(n)$ to be positive for small n and negative for large n. Simply set $f(n) = r - sn$ to give

$$\frac{dn}{dt} = n(r - sn).$$

A deterministic model

$$\frac{dn}{dt} = nf(n).$$

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

We want $f(n)$ to be positive for small n and negative for large n. Simply set $f(n) = r - sn$ to give

$$\frac{dn}{dt} = n(r - sn).$$

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)

The Verhulst model

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.

The Verhulst model

MATHÉMATIQUE ET PHYSIQUE. 117

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	29,981,336 208,231	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

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 $s = r/K$.

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 $s = r/K$.

Integration gives

$$n_t = \frac{K}{1 + \left(\frac{K - n_0}{n_0}\right) e^{-rt}} \qquad (t \geq 0).$$

Verhulst-Pearl model

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.

Verhulst-Pearl model

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

Pearl was a “social drinker”

Pearl was widely known for his lust for life and his love of food, drink, music and parties. He was a key member of the Saturday Night Club. Prohibition made no dent in Pearl’s drinking habits (which were legendary).

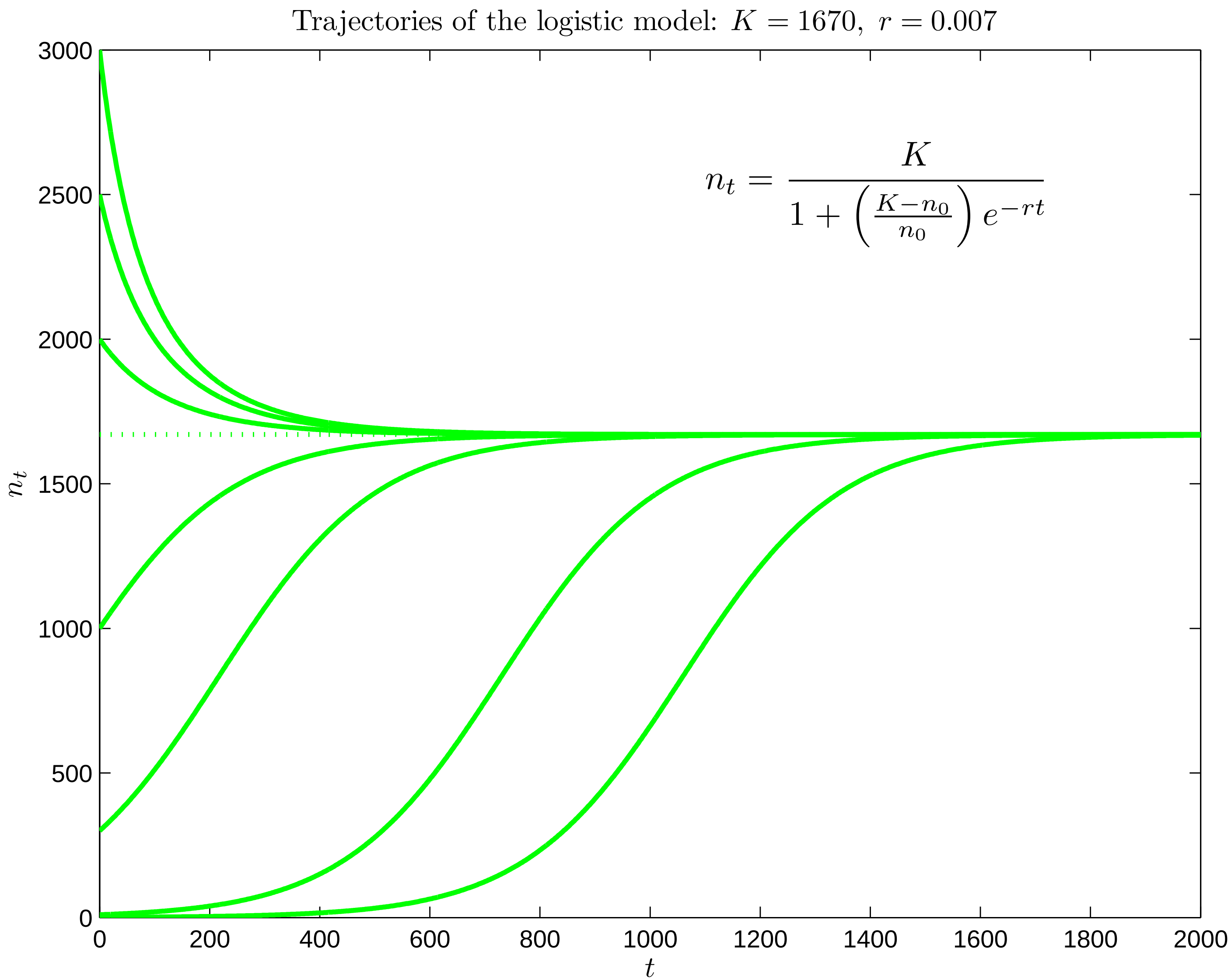
Pearl was a “social drinker”

Pearl was widely known for his lust for life and his love of food, drink, music and parties. He was a key member of the Saturday Night Club. Prohibition made no dent in Pearl’s drinking habits (which were legendary).

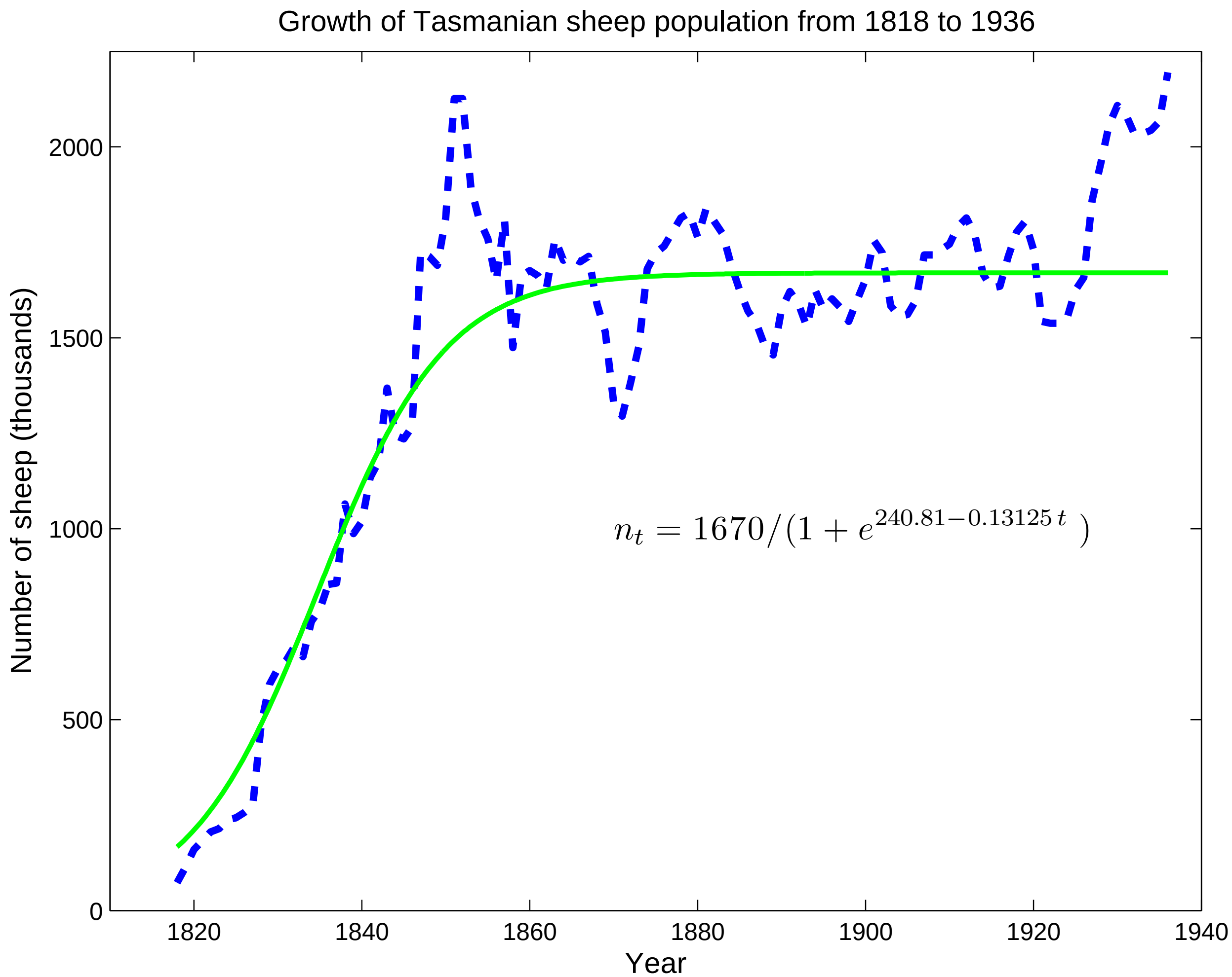
In 1926, his book, Alcohol and Longevity, demonstrated that drinking alcohol in moderation is associated with greater longevity than either abstaining or drinking heavily.

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

Verhulst-Pearl model

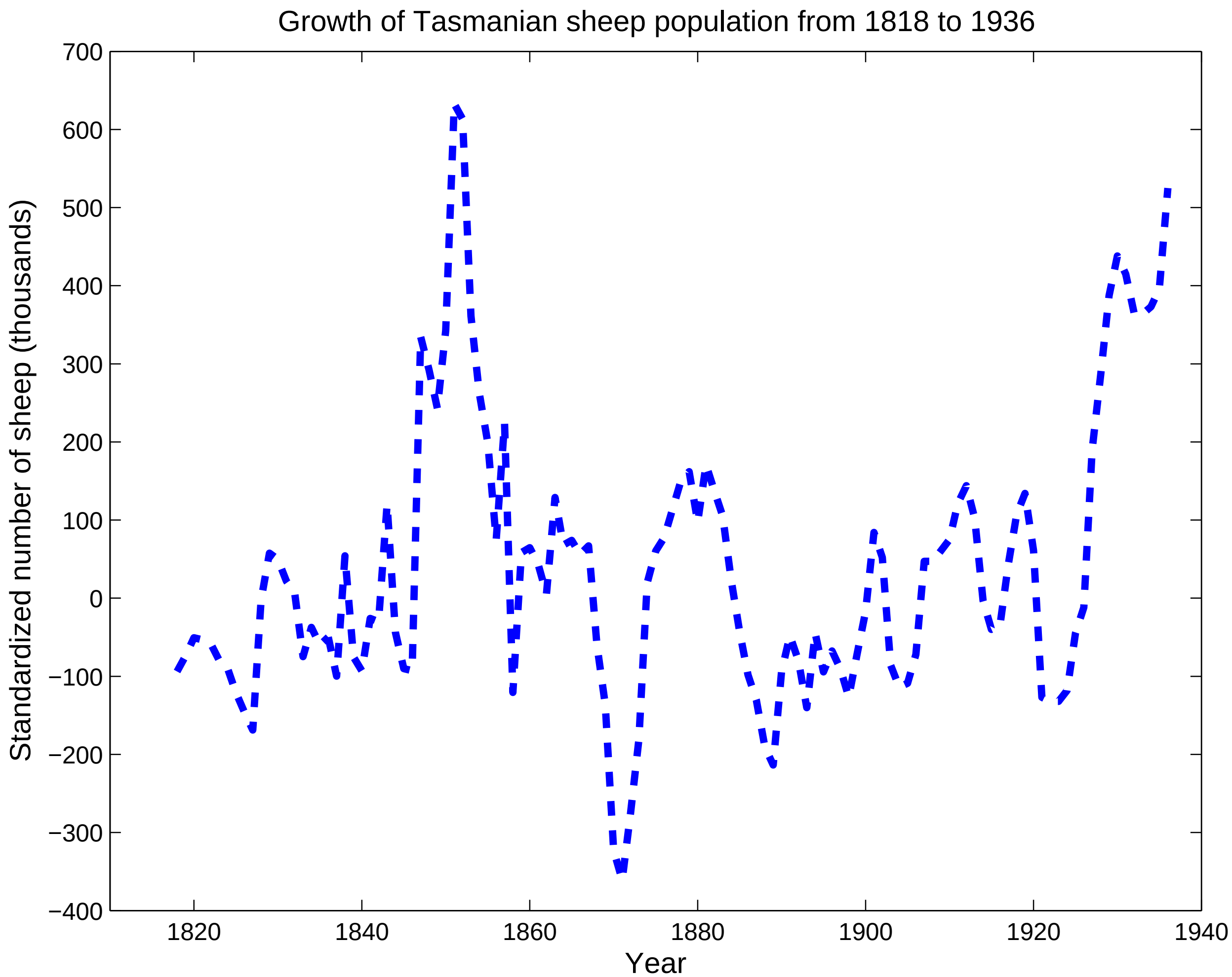


Sheep in Tasmania



Davidson, J. (1938) On the growth of the sheep population in Tasmania, Trans. Roy. Soc. Sth. Austral. 62, 342–346.

Sheep in Tasmania



(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:

> "I suspect that the world is not deterministic - I should add some noise"

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:

> "I suspect that the world is not deterministic - I should add some noise"

*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're a mile away and you have their shoes.

Adding noise

In our case,

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

or perhaps

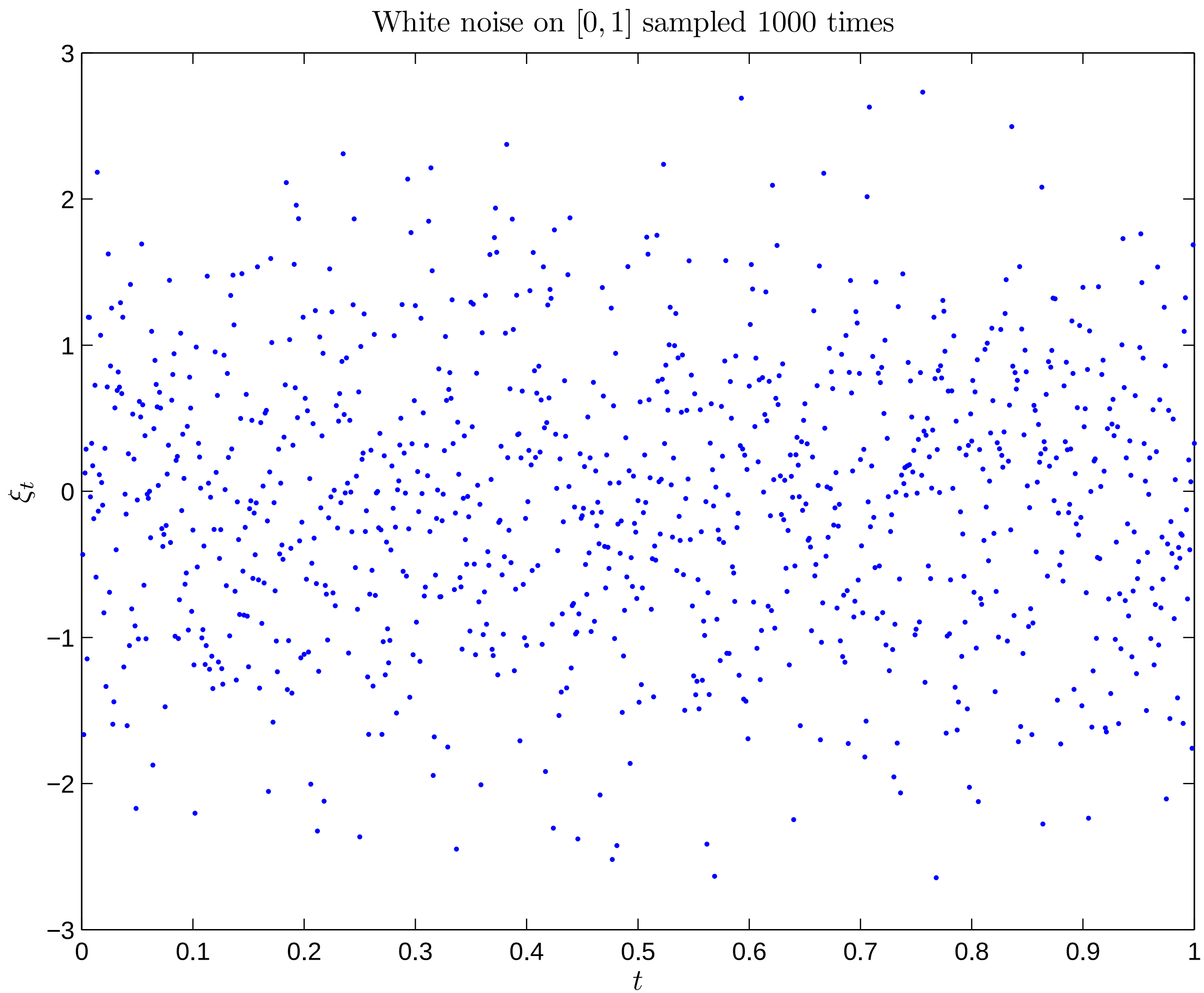
$$\frac{dn}{dt} = rn\left(1 - \frac{n}{K}\right) + \sigma \times \text{noise}.$$

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



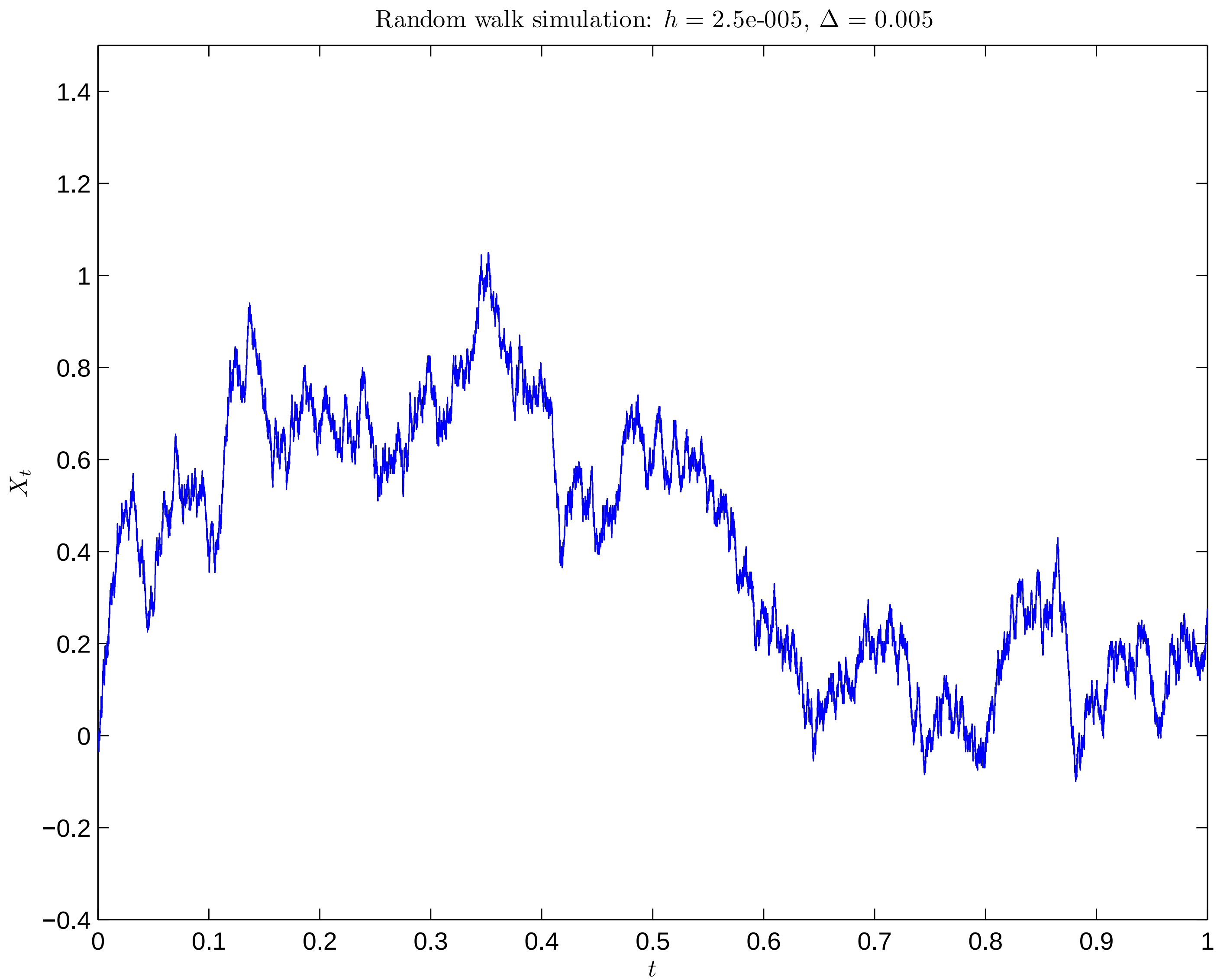
White noise on $[0, 1]$ sampled 1000 times
3
2
1
0
−1
−2
−3
ξ_t
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
t

Brownian motion

The white noise process $(\xi_t,\, t \geq 0)$ is formally 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. If $\Delta \sim \sqrt{h}$, as $h \to 0$, then the limit process is *standard Brownian motion*.

Symmetric random walk: $\Delta = \sqrt{h}$



Brownian motion

The white noise process $(\xi_t,\, t \geq 0)$ is formally 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. If $\Delta \sim \sqrt{h}$, as $h \to 0$, then the limit process is *standard Brownian motion*.

Brownian motion

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 $\mathrm{Cov}(dB_t, dB_s) = 0 \ (s \neq t)$.

Brownian motion

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 $\mathrm{Cov}(dB_t, dB_s) = 0 \ (s \neq t)$.

The correct interpretation is by way of the Itô integral:

$$B_t = \int_0^t dB_s = \int_0^t \xi_s \, ds.$$

Brownian motion

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

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

This *stochastic differential equation (SDE)* can be integrated to give $W_t = \mu t + \sigma B_t$.

Brownian motion

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

This *stochastic differential equation (SDE)* can be integrated to give $W_t = \mu t + \sigma B_t$.

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

$$dn_t = r n_t \left(1 - n_t/K\right) dt + \sigma dB_t$$

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.]

Langevin

Langevin introduced a “stochastic force” (his phrase “complementary force”–complimenting the viscous drag μ) pushing the Brownian particle around in velocity space (Einstein worked in configuration space).

Langevin

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

$$dv_t = -\mu v_t \, dt + \sigma dB_t.$$

This is Newton's law ($-\mu v =$ Force $= m\dot{v}$) *plus* noise.

Langevin

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

$$dv_t = -\mu v_t \, dt + \sigma dB_t.$$

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

Langevin

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

$$dv_t = -\mu v_t \, dt + \sigma dB_t.$$

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

Warning: $\int_0^t v_s \, ds \neq B_t$; this functional is not even Markovian.

Langevin

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*.

Langevin was a dark horse

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

Langevin was a dark horse

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

The person on the right is not Langevin, but Langevin's PhD supervisor *Pierre Curie*.

Solution to Langevin's equation

To solve $dv_t = -\mu v_t \, dt + \sigma dB_t$, consider the process $y_t = v_t e^{\mu t}$.

Solution to Langevin's equation

To solve $dv_t = -\mu v_t \, dt + \sigma dB_t$, consider the process $y_t = v_t e^{\mu t}$. Differentiation (Itô calculus!) gives $dy_t = e^{\mu t} dv_t + \mu e^{\mu t} v_t dt$.

Solution to Langevin's equation

To solve $dv_t = -\mu v_t\, dt + \sigma dB_t$, consider the process $y_t = v_t e^{\mu t}$. Differentiation (Itô calculus!) gives $dy_t = e^{\mu t} dv_t + \mu e^{\mu t} v_t dt$.

But, from Langevin's equation we have that

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

Solution to Langevin's equation

To solve $dv_t = -\mu v_t\, dt + \sigma dB_t$, consider the process $y_t = v_t e^{\mu t}$. Differentiation (Itô calculus!) gives $dy_t = e^{\mu t} dv_t + \mu e^{\mu t} v_t dt$.

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

Solution to Langevin's equation

To solve $dv_t = -\mu v_t\, dt + \sigma dB_t$, consider the process $y_t = v_t e^{\mu t}$. Differentiation (Itô calculus!) gives $dy_t = e^{\mu t} dv_t + \mu e^{\mu t} v_t dt$.

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 $dy_t = \sigma e^{\mu t} dB_t$. Integration gives

$$y_t = y_0 + \int_0^t \sigma e^{\mu s} dB_s,$$

Solution to Langevin's equation

To solve $dv_t = -\mu v_t \, dt + \sigma dB_t$, consider the process $y_t = v_t e^{\mu t}$. Differentiation (Itô calculus!) gives $dy_t = e^{\mu t} dv_t + \mu e^{\mu t} v_t dt$.

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 $dy_t = \sigma e^{\mu t} dB_t$. Integration gives

$$y_t = y_0 + \int_0^t \sigma e^{\mu s} dB_s,$$

and so (the *Ornstein-Uhlenbeck process*)

$$v_t = v_0 e^{-\mu t} + \int_0^t \sigma e^{-\mu(t-s)} dB_s.$$

Solution to Langevin's equation

The Ornstein-Uhlenbeck process:

$$v_t = v_0 e^{-\mu t} + \int_0^t \sigma e^{-\mu(t-s)} dB_s.$$

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:

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

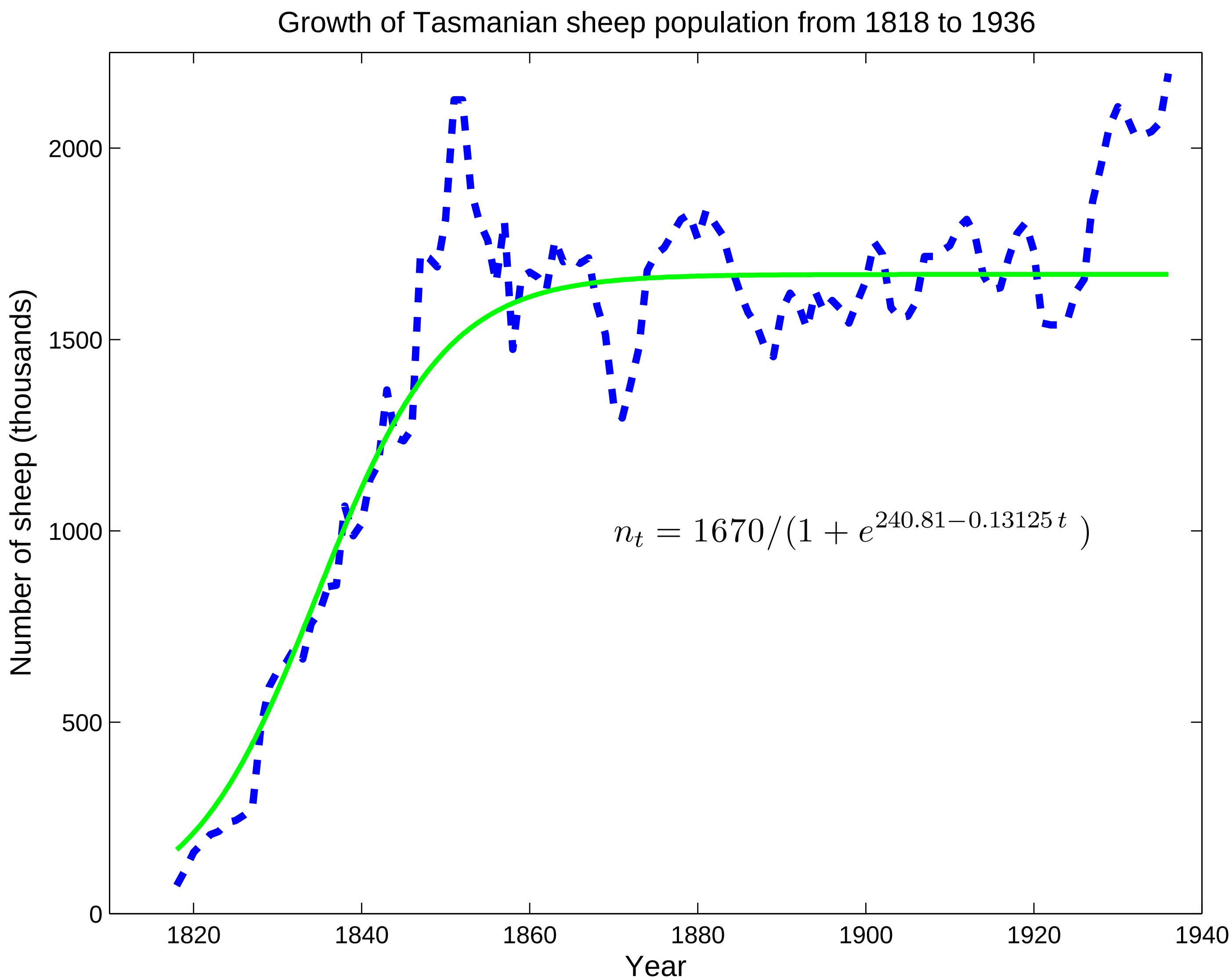
Where were we?

We had just added noise to our logistic model:

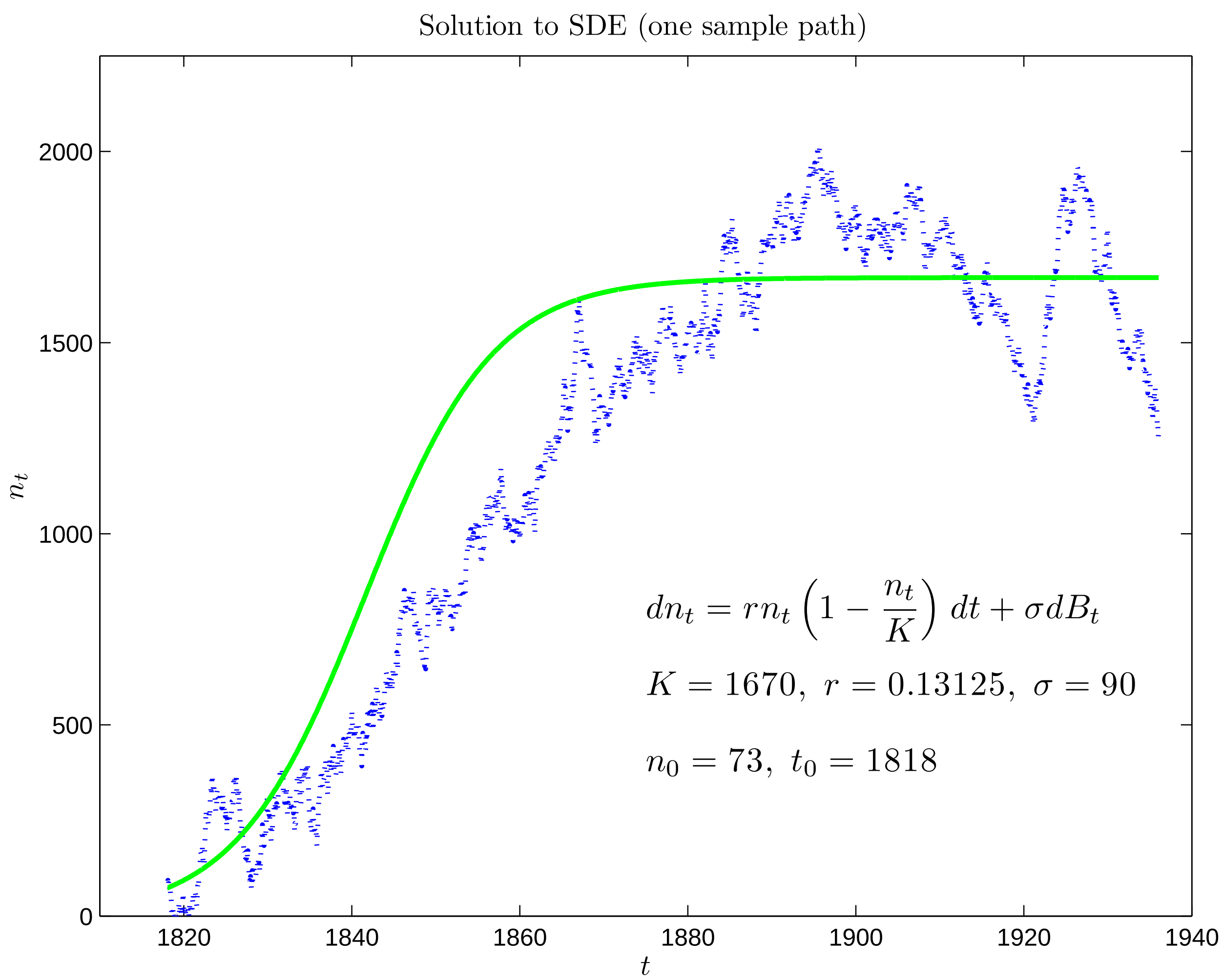
$$dn_t = rn_t\left(1 - \frac{n_t}{K}\right)dt + \sigma\, dB_t. \tag{1}$$

So, what is wrong with (1)?

Sheep in Tasmania

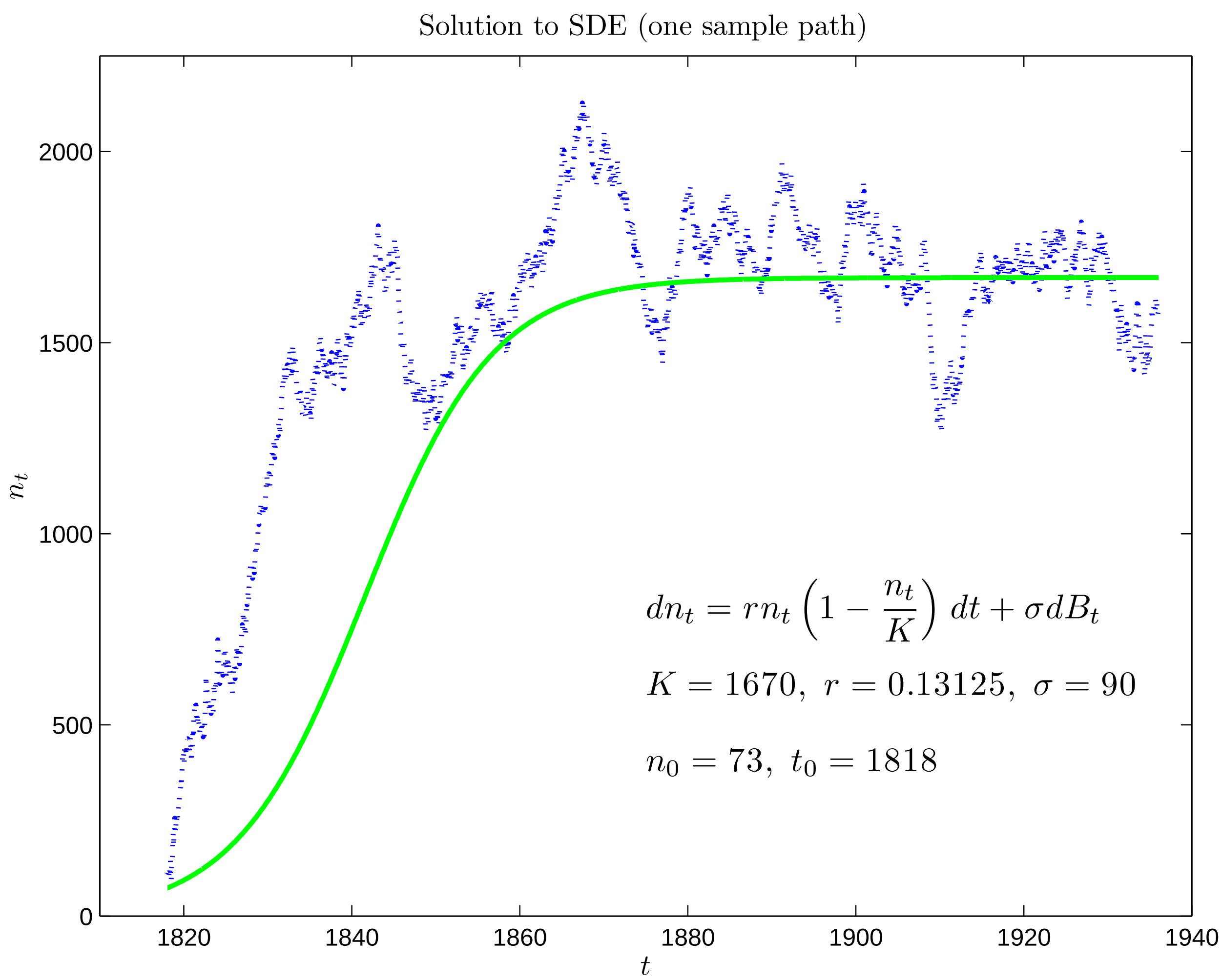


Solution to SDE (Run 1)



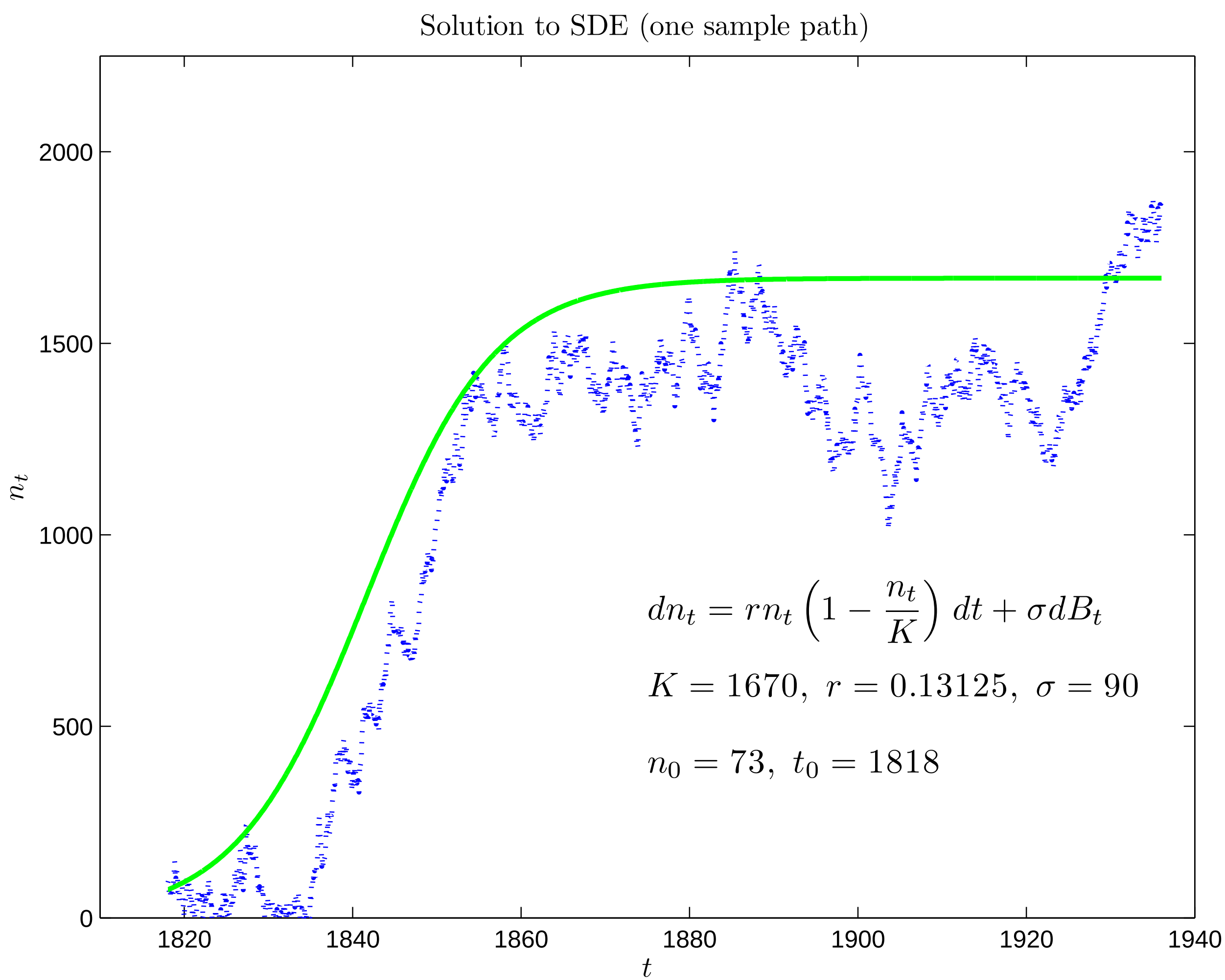
(Solution to the deterministic model is in green)

Solution to SDE (Run 2)



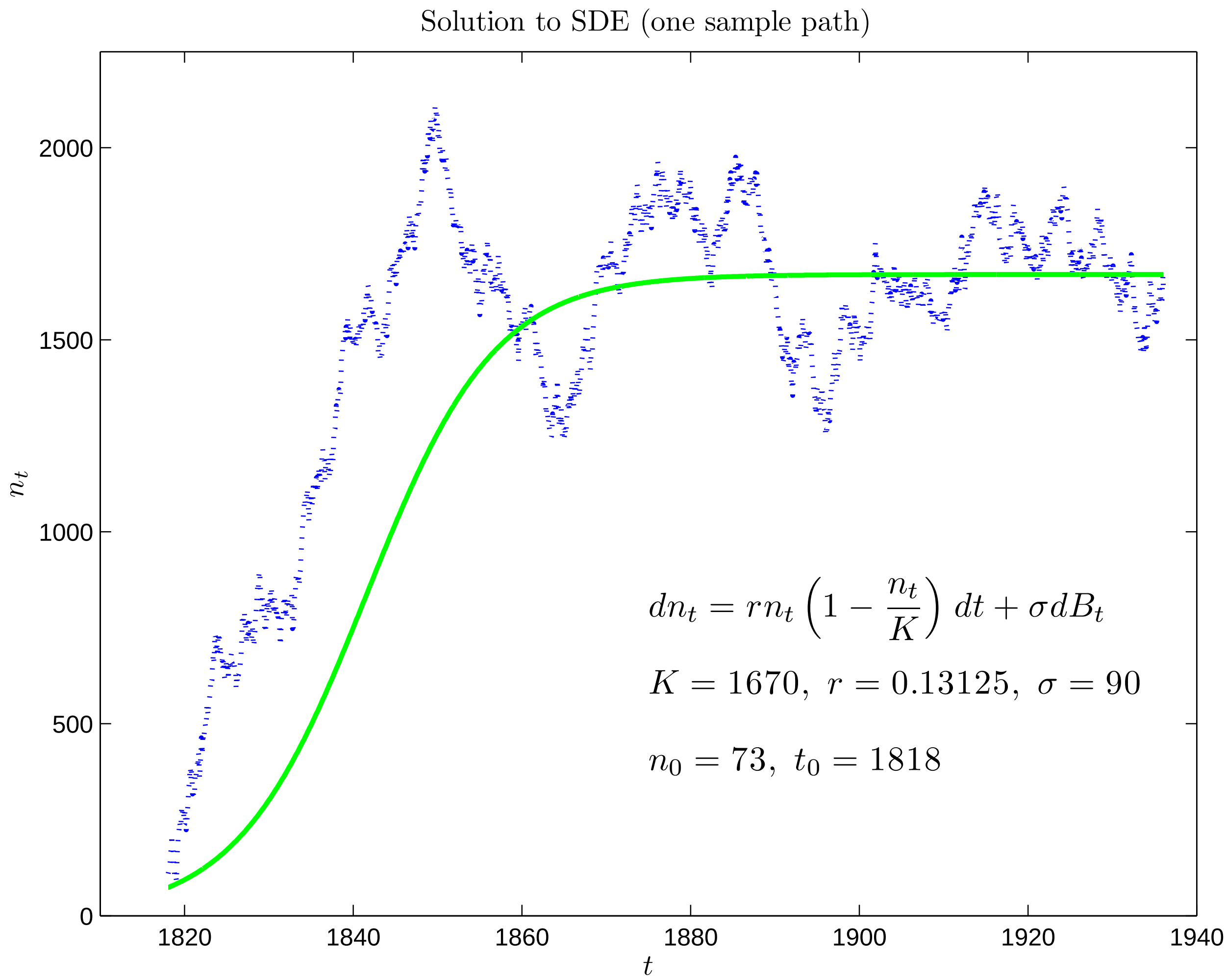
(Solution to the deterministic model is in green)

Solution to SDE (Run 3)



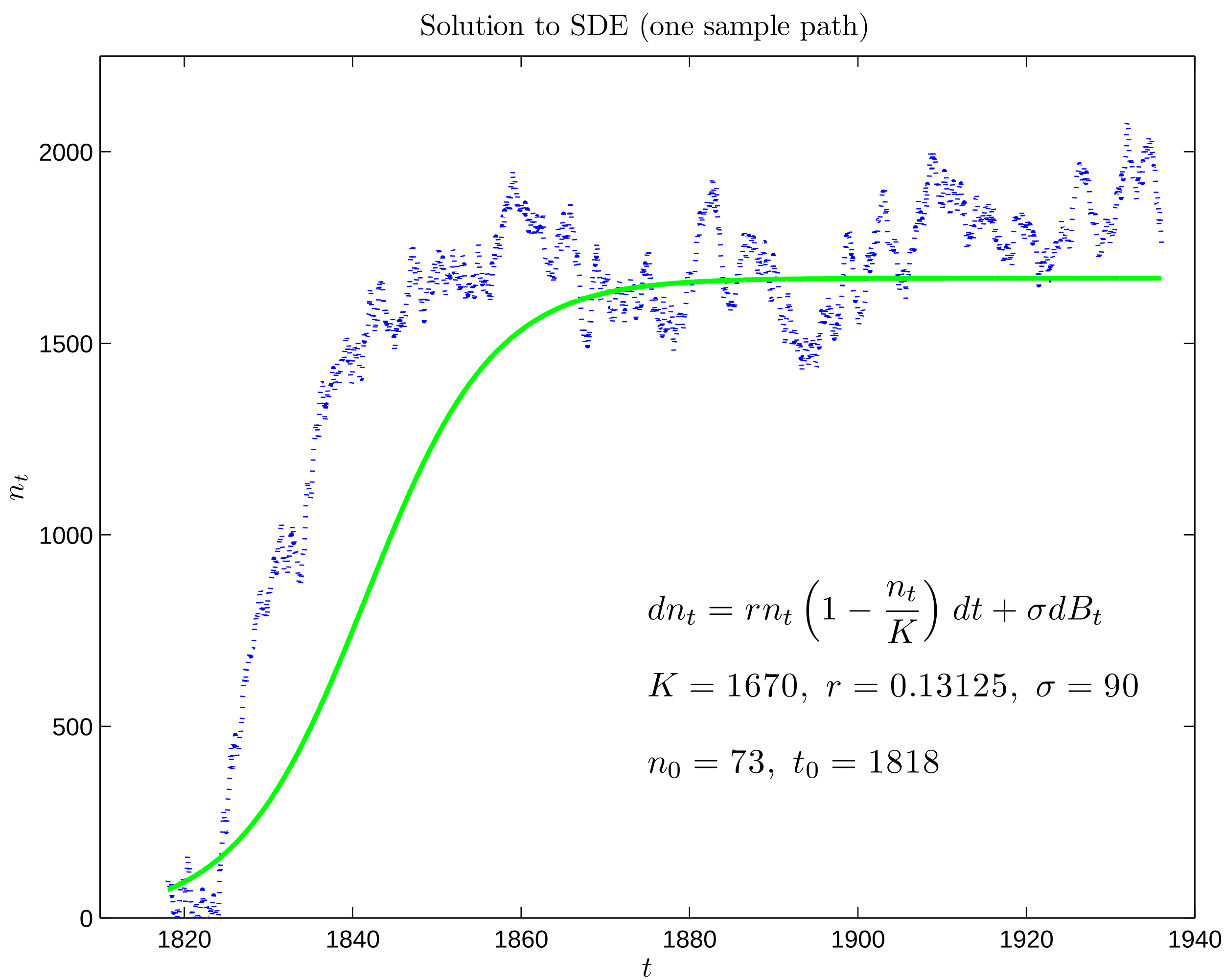
(Solution to the deterministic model is in green)

Solution to SDE (Run 4)



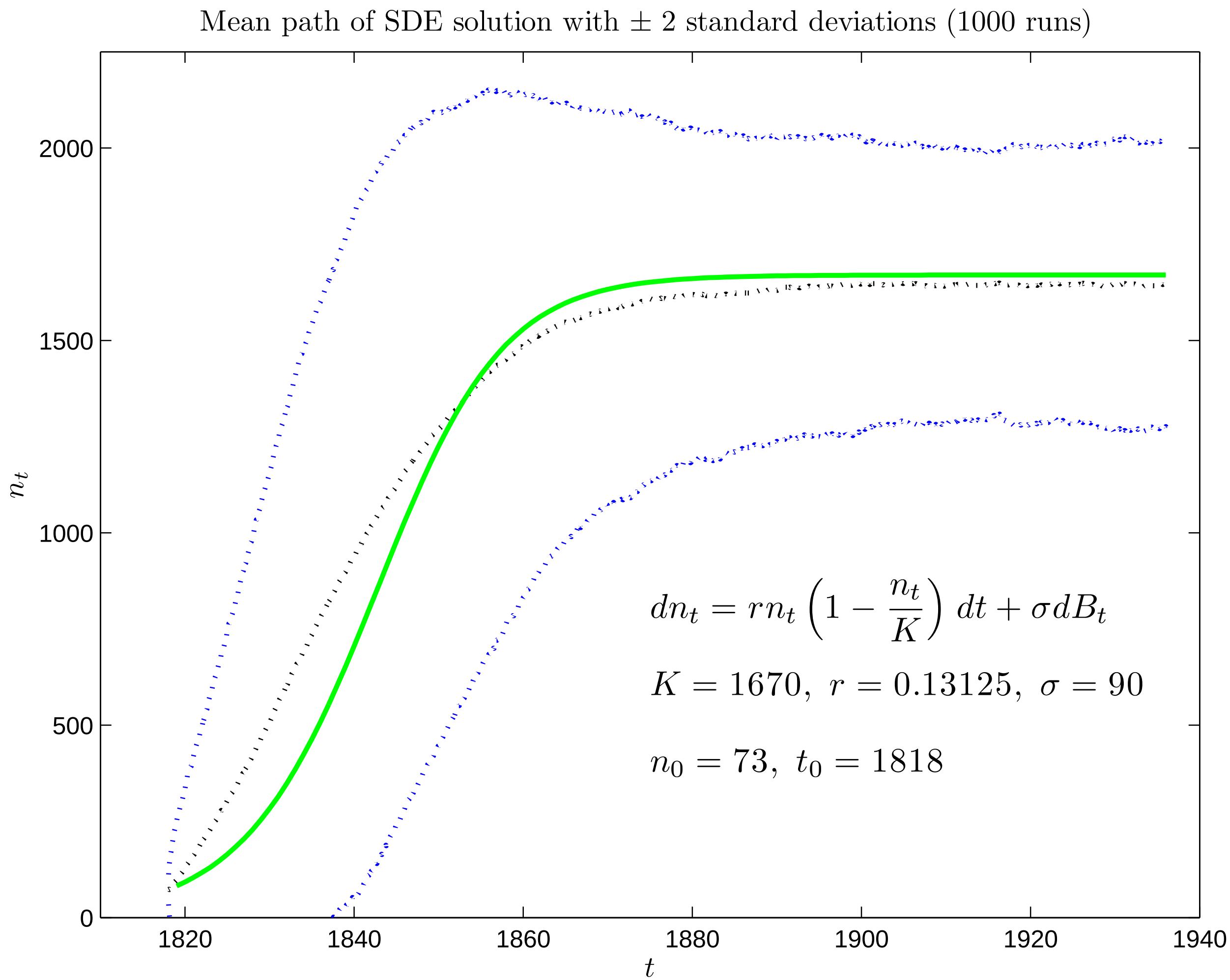
(Solution to the deterministic model is in green)

Solution to SDE (Run 5)



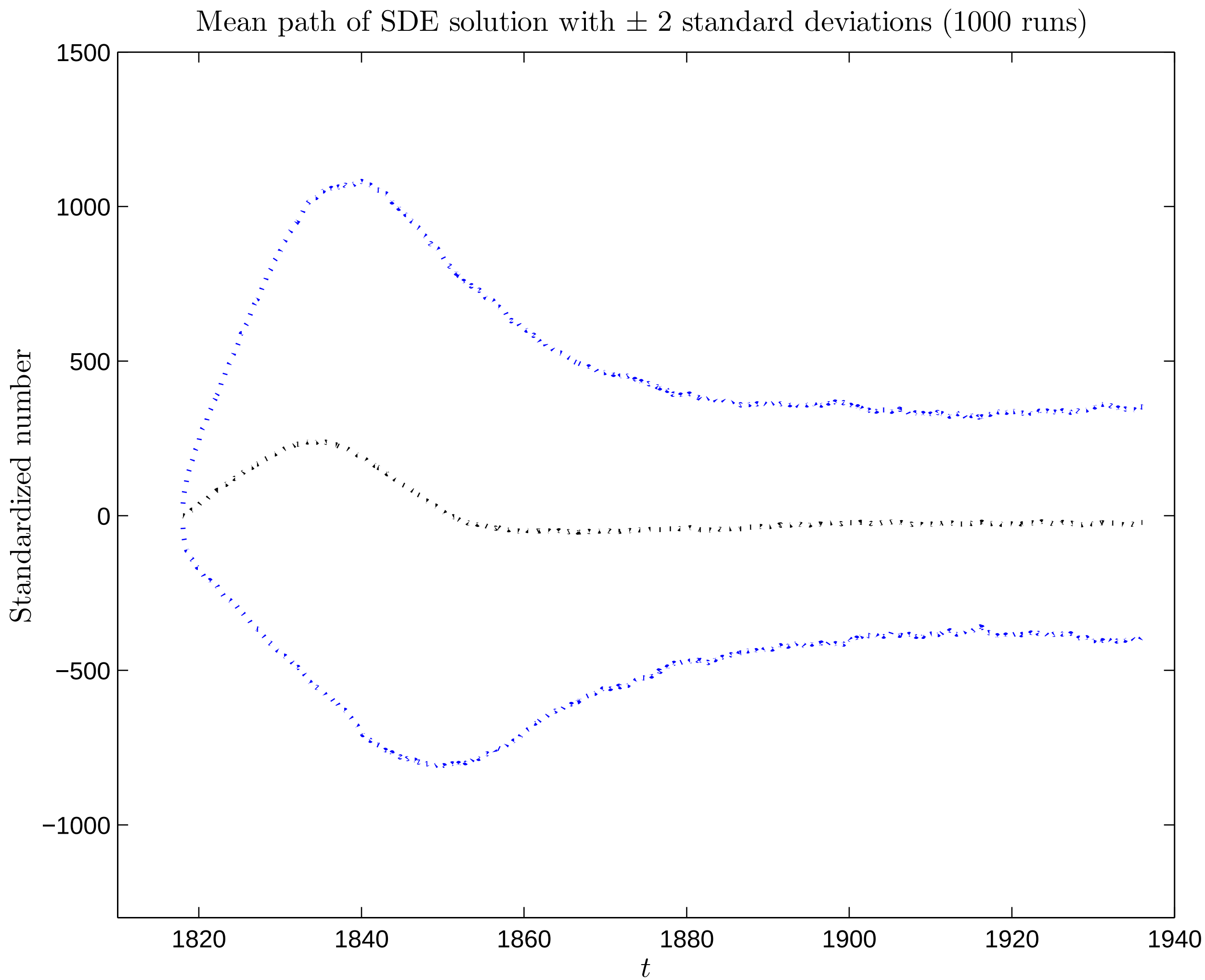
(Solution to the deterministic model is in green)

Solution to SDE



(Solution to the deterministic model is in green)

Solution to SDE



(With the solution to the deterministic model subtracted)

Logistic model with noise

So, what is wrong with the model?

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

Logistic model with noise

So, what is wrong with the model?

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

For a start:

Logistic model with noise

So, what is wrong with the model?

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

For a start:

- 0 is *reflecting*;

Logistic model with noise

So, what is wrong with the model?

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

For a start:

- 0 is *reflecting*;
- The mean path of the SDE solution does not follow a logistic curve;

Logistic model with noise

So, what is wrong with the model?

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

For a start:

- 0 is *reflecting*;
- The mean path of the SDE solution does not follow a logistic curve;
- The variance in the solution is large for the non-equilibrium phase – is this okay?

Logistic model with noise

So, what is wrong with the model?

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

For a start:

- 0 is *reflecting*;
- The mean path of the SDE solution does not follow a logistic curve;
- The variance in the solution is large for the non-equilibrium phase – is this okay?

$\ldots$ not to mention the fact that n_t is a continuous variable, yet population size is an integer-valued process!

The variance!

Since the variance is not uniform over time, we should *at least* have

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

if not

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