Vector-borne Disease Control &
Taylor's Law of Fluctuation Scaling:
Chagas Disease in Argentina

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Montpellier, France, 2019-09-10

Villefort, Cévennes, France 20190904
Outline

1. Taylor’s law (TL)
2. Empirical examples
3. Empirical counterexamples
4. Chagas disease & TL
5. Spraying insecticides & TL
6. Using TL for more efficient fixed-precision estimation of insect vector populations
### TL data structure: multiple samples, each with multiple observations

<table>
<thead>
<tr>
<th>Sample number</th>
<th>(j=1)</th>
<th>(j=2)</th>
<th>(j=3)</th>
<th>(j=\ldots)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population size or density in units (quadrats, plots, transects, counties, states, years, days)</td>
<td>(x_{11})</td>
<td>(x_{12})</td>
<td>(x_{13})</td>
<td>(x_{1\ldots})</td>
</tr>
<tr>
<td></td>
<td>(x_{21})</td>
<td>(x_{22})</td>
<td>(x_{23})</td>
<td>(x_{2\ldots})</td>
</tr>
<tr>
<td></td>
<td>(x_{31})</td>
<td>(x_{32})</td>
<td>(x_{33})</td>
<td>(x_{3\ldots})</td>
</tr>
<tr>
<td></td>
<td>(x_{41})</td>
<td>(x_{42})</td>
<td>(x_{43})</td>
<td>(x_{4\ldots})</td>
</tr>
<tr>
<td></td>
<td>(x_{51})</td>
<td>(x_{52})</td>
<td>(x_{53})</td>
<td>(x_{5\ldots})</td>
</tr>
<tr>
<td>Mean (weighted)</td>
<td>(m_1)</td>
<td>(m_2)</td>
<td>(m_3)</td>
<td>(m_{\ldots})</td>
</tr>
<tr>
<td>Variance (weighted)</td>
<td>(v_1)</td>
<td>(v_2)</td>
<td>(v_3)</td>
<td>(v_{\ldots})</td>
</tr>
</tbody>
</table>
Japanese beetle larvae \( v_j = am_j^b \)

Chester I. Bliss *J. of Economic Entomology* 1941

Areas 1, 3:
144 samples each area,
each sample
16 counts of 1 sq.ft. each

Areas 2, 4:
144 samples each area,
each sample
16 counts of 1 sq.ft. each
Taylor’s law *Nature* 1961

In multiple sets of samples, the variance of population density is proportional to a power of the mean population density.

\[
\text{variance} = a(\text{mean})^b, \quad a > 0.
\]

\[
\log(\text{variance}) = \log(a) + b \cdot \log(\text{mean}).
\]

\[
\frac{\text{variance}}{(\text{mean})^b} = a, \quad a > 0.
\]

Taylor stated no model of error (deviations from exact equality).

Lionel Roy Taylor (1924–2007)
<table>
<thead>
<tr>
<th>Name</th>
<th>Description</th>
<th>County</th>
<th>Unit</th>
<th>Coarse</th>
<th>Fine</th>
<th>Water</th>
<th>Woody</th>
<th>Herb</th>
<th>Grassy</th>
<th>Vegetation</th>
<th>Animal</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Shellfish on seashore, <em>Tellina testa</em> da Costa, <em>Eulamellibranchia</em></td>
<td>Sand, 83 units, various sites</td>
<td></td>
<td></td>
<td>83%</td>
<td>17%</td>
<td>0%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 European chafer larve, <em>Anaphthalmus majalis</em></td>
<td>Pasture soil, 25 units, each 1 ft. sq.</td>
<td></td>
<td></td>
<td>25%</td>
<td>75%</td>
<td>0%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 Flying insects, various orders: <em>Insecta</em></td>
<td>Insecta</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 Wireworms, <em>Agrilus spp.</em></td>
<td>Arable land soil, 175 units, each 1 ft. sq.</td>
<td></td>
<td></td>
<td>175%</td>
<td>0%</td>
<td>0%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5 Gall midge larve, <em>Saprinella melolontha</em></td>
<td>Pier foliage, 25 units, larve/wig</td>
<td></td>
<td></td>
<td>25%</td>
<td>75%</td>
<td>0%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6 Wireworms, <em>Limonius</em> spp., <em>Coleoptera</em>; <em>Insecta</em></td>
<td>Bean leaves, 4 units, lesions/half leaf</td>
<td></td>
<td></td>
<td>4%</td>
<td>96%</td>
<td>0%</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>7 Spruce budworm larve, <em>Choristoneura fumiferana</em> (Clem.), <em>Lepidoptera</em></td>
<td>Potato foliage, 8,304 counts: insect/2 ft.</td>
<td></td>
<td></td>
<td>83%</td>
<td>17%</td>
<td>0%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8 Galls on trees, various species</td>
<td>Water, net collection, side count, 10 areas</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9 Virus disease, tobacco necrosis virus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10 Colorado beetle adults, <em>Leptinotarsa decemlineata</em>, <em>Sav.</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>11 Japanese beetle larve, <em>Popillia japonica</em> New., <em>Coleoptera</em>: <em>Insecta</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 Macro-zooplankton</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>
TL matters practically because variability is fundamental.

- Fluctuations of forests, fisheries, infectious diseases, disease vectors, tornados
- Conservation of endangered species
- Sampling insect pests of cotton & soybeans, fishery stocks
- Linking levels of biological organization: variance-body mass allometry
- Evaluation of human population projections
Slope $b$ in TL is "elasticity."

Taylor's law says: variance $\approx a(\text{mean})^b$.

Then $b \approx \frac{d \log \text{variance}}{d \log \text{mean}} = \frac{1}{\text{var}} \times d \text{ var} = \frac{1}{\text{mean}} \times d \text{ mean}

\approx \% \text{ change in variance for 1\% change in mean.}$

$b = "\text{elasticity of variance with respect to mean" (in economists' use of "elasticity").}$

$b = 2$ iff coefficient of variation (SD/mean) & signal-to-noise ratio (mean/SD) are the same for all values of the mean.
Spatial & temporal Taylor’s laws

Suppose we measure population density at $s$ in space & at $t$ in time.

Spatial TL: for each $t$, mean & variance average over space $s$.

Temporal TL: for each $s$, mean & variance average over time $t$. 
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Competing bacteria satisfy spatial TL with slope $\approx 2$

Ramsayer, Fellous, Cohen, Hochberg *Biology Letters* 2011; 8 replicates per treatment

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![Graphs showing the relationship between log(variance) and log(mean) for Pseudomonas fluorescens and Serratia marcescens.](image)

- ○, ---, - - - alone
- •, —— competing

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Michael Hochberg
20120323 Arthurs Pass, New Zealand
New Zealand mountain beech

Cohen, Lai, Coomes, Allen, Oikos 2016
3 spatial scales: subplots 5x5m, plots 20x20m, blocks
16 subplots/plot, 5-33 plots/block, 13 blocks

10 censuses over 30 years
New Zealand mountain beech

David Coomes
2013

10 censuses
1974-2004
TL slope $b$ is much greater at larger spatial scale than small. Slope cannot be species-specific characteristic.


3 < $b$ < 4 for 20m x 20m plots in blocks.

1 < $b$ < 2 for 5m x 5m subplots in plots.
Norway: spatial mean & spatial variance of people/km$^2$ in 18 counties excluding Oslo

slope 2.75 (2.72, 2.78)

1978 (A) – 2010 (g)
Age-specific death rates, France
Human Mortality Database

<table>
<thead>
<tr>
<th>Year $t$</th>
<th>Age $x$</th>
<th>0</th>
<th>1</th>
<th>$x$</th>
<th>100</th>
</tr>
</thead>
<tbody>
<tr>
<td>1960</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>1961</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$t$</td>
<td></td>
<td></td>
<td></td>
<td>$m_{t,x} = \frac{d_{t,x}}{L_{t,x}}$</td>
<td></td>
</tr>
<tr>
<td>2008</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2009</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td></td>
<td>Mean($x$)</td>
<td></td>
</tr>
<tr>
<td>Variance</td>
<td></td>
<td></td>
<td></td>
<td>Var($x$)</td>
<td></td>
</tr>
</tbody>
</table>
Female death rates for each year of age, mean & variance over 1960-2009, France

Bohk, Rau, Cohen, *Demog. Research* 2015
Male death rates for each year of age, mean & variance over 1960-2009, France

Bohk, Rau, Cohen, *Demog. Research* 2015
Female death rates by age, mean & variance over time 1960-2009

Bohk, Rau, Cohen, Demographic Research 2015
Male death rates by age, mean & variance over time 1960-2009
Bohk, Rau, Cohen, *Demographic Research* 2015
F1+ tornadoes per outbreak in USA: variance~(mean)$^{4.3}$


![Graphs showing the relationship between mean and variance of tornadoes per outbreak over time.](image)

**Variance of # of tornadoes per outbreak rises >4 x as fast as mean.**
Higher percentiles increased faster. “quantile regression”

(a) Percentiles of tornadoes per outbreak

(b) Linear growth rate

Tippett, Lepore, Cohen Science 2016
Extreme outbreaks (12+ tornadoes) increased extremely.

“Once in 5 years” extreme outbreak increased from 40 tornadoes in 1965 to 80 tornadoes in 2015.

“Once in 25 years” extreme outbreak more than doubled from 1965 to 2015.

Tippett, Lepore, Cohen Science 2016
Metazoan population density (individuals m\(^{-2}\)) obey spatial TL. Parameters differ by life style.

Lagrue, Poulin, Cohen PNAS 2015

First demonstration that the parameters of TL depend on lifestyle within a given metazoan community

A. free-living unparasitized: b=1.68 (1.64, 1.72)
B. free-living parasitized: b=2.02 (1.97, 2.06)
C. parasitic: b=2.10 (2.06, 2.15)
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Quadratic model beats Taylor's law for parasite number per host.

\( \log_{10} \) variance of parasites per host

\( \log_{10} \) mean parasites per host

Parasites/host follow negative binomial: variance=mean+2(mean^2).

Minimum sample size = 5

Minimum sample size = 15
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Chagas disease
Carlos Chagas discovered infectious agent 1909

Estimated global population infected by *Trypanosoma cruzi*, 2009

WHO 2016-03
6-7 million cases of Chagas disease 2019

Distribution of cases of *Trypanosoma cruzi* infection, based on official estimates and status of vector transmission, worldwide, 2006–2009
Parasite & vectors are widespread.

Parasite: *Trypanosoma cruzi*

Vectors: multiple species, mainly *Triatoma infestans*

Source: http://www.cpqrr.fiocruz.br/laboratorios/lab_triato/TriatoInfestans.html
Triatomine bug needs a blood meal to moult & lay eggs.

https://www.cdc.gov/parasites/images/chagas/triatomine_stages_lg.jpg

Distribución aparente de *Triatoma infestans*

Homes & out-buildings are built of mud, sticks, & thatch, ideal for bugs. Prov. Santiago del Estero, NW Argentina

Chagas' disease
Bug bites dog infected with *T. cruzi*, infected bug bites boy.
Each habitat (domicile, chicken coop, goat corral, granary) defines one sample.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>$x_{11}$</th>
<th>$x_{12}$</th>
<th>$x_{13}$</th>
<th>$x_{...}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bug population density (per hour of search) in exemplars of this habitat</td>
<td>$x_{21}$</td>
<td>$x_{22}$</td>
<td>$x_{23}$</td>
<td>$...$</td>
</tr>
<tr>
<td></td>
<td>$x_{31}$</td>
<td>$x_{32}$</td>
<td>$x_{33}$</td>
<td>$...$</td>
</tr>
<tr>
<td></td>
<td>$x_{41}$</td>
<td>$x_{42}$</td>
<td>$x_{43}$</td>
<td>$...$</td>
</tr>
<tr>
<td></td>
<td>$x_{51}$</td>
<td>$x_{52}$</td>
<td>$...$</td>
<td>$...$</td>
</tr>
<tr>
<td>Mean</td>
<td>$m_{1}$</td>
<td>$m_{2}$</td>
<td>$m_{3}$</td>
<td>$m_{...}$</td>
</tr>
<tr>
<td>Variance</td>
<td>$v_{1}$</td>
<td>$v_{2}$</td>
<td>$v_{3}$</td>
<td>$v_{...}$</td>
</tr>
</tbody>
</table>

Cohen, Rodríguez-Planes, Gaspe, Cecere, Cardinal, Gürtler, *PLoS Neglected Tropical Diseases* 2017

Cohen, Rodríguez-Planes, Gaspe, Cecere, Cardinal, Gürtler, *PLoS Neglected Tropical Diseases* 2017
Figueroa: Vectors of Chagas disease obey spatial TL.

Cohen, Rodríguez-Planes, Gaspe, Cecere, Cardinal, Gürtler, PLoS Neglected Tropical Diseases 2017
Uses of TL in Chagas vector control

Flagging errors in data
Identifying habitats of unusually high or unusually low variability
Designing sequential sampling to reach specified precision, using stopping line derived from TL
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Suppose TL holds before the house compounds (including all (peri)domestic structures) are sprayed with insecticides to kill the vectors: for relative population density of a single vector species,

\[ \log \text{variance} = \log a + b \log \text{mean}. \]

What would be the effect of spraying? Would TL hold after spraying? If so, with what intercept and slope?
Model of spraying & TL: notation
Cohen, Gürtler et al., PLoS NTD 2017

Habitats are labeled $h = 1, 2, \ldots, H$.

$B(h) = \text{random number of vectors of one } Triatoma \text{ species in the various sites of habitat } h \text{ in study area Before spraying.}$

$A(h) = \text{random number of vectors of one } Triatoma \text{ species in the various sites of habitat } h \text{ in study area After spraying.}$

Assume $\log_{10} \text{Var}(B(h))$

$= \log_{10} a + b \log_{10} E(B(h)), \ h = 1, 2, \ldots, H.$
Model of spraying & TL: key assumptions, key result

Suppose that a fraction $s$, $0 < s < 1$, of vectors survive spraying in every site of every habitat. $s = \text{Survive Spraying}$.

If $\log_{10} \text{Var}(B(h)) = \log_{10} a + b \log_{10} E(B(h))$, then $\log_{10} \text{Var}(A(h)) = \log_{10} a + (2-b) \log_{10} s + b \log_{10} E(A(h))$, $h = 1, 2, ..., H$.

After spraying, TL holds for the relative population density of vectors with the same exponent $b$ as before spraying. Intercept changes, but little if $b \approx 2$ or $s \approx 1$. 52
Olta: Vectors of Chagas disease obey spatial TL before (black) & after (red) community-wide spraying.

Cohen, Rodríguez-Planes, Gaspe, Cecere, Cardinal, Gürtler, PLoS Neglected Tropical Diseases 2017
Direct tests of model of spraying for *T. infestans*

Cohen, Rodríguez-Planes, Gaspe, Cecere, Cardinal, Gürtler, *PLoS Neglected Tropical Diseases* 2017
Slope $b$ in TL is independent of scale of measurement.

If $s^2 = am^b$ for r.v. $X$, & $Y = kX, k > 0$, then mean of $Y$ is $\mu = km$, variance of $Y$ is

$$\sigma^2 = k^2 s^2 = k^2 am^b = k^2 a \left( \frac{\mu}{k} \right)^b = k^{2-b} a \mu^b.$$ 

$Y$ obeys TL power law with same exponent $b$, coefficient $a k^{2-b}$. 

2019-09-10 Joel E. Cohen
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Using TL to design sampling with fixed precision

Suppose we collect multiple samples on each day of a sequence of days $t = 1, 2, \ldots$

We want to stop sampling when the mean population density can be estimated with a fixed "precision" defined as

$$C = \frac{\text{standard deviation of mean density}}{\text{mean density}}.$$  

$C = 0.1$ when std. dev. of mean density (SEM) is 10% of mean density.
Data structure: multiple samples, each with multiple observations

<table>
<thead>
<tr>
<th>Sample day</th>
<th>$t=1$</th>
<th>$t=2$</th>
<th>$t=3$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of individuals in samples on day $t$</td>
<td>$x_{11}$</td>
<td>$x_{12}$</td>
<td>$x_{13}$</td>
</tr>
<tr>
<td></td>
<td>$x_{21}$</td>
<td>$x_{22}$</td>
<td>$x_{23}$</td>
</tr>
<tr>
<td></td>
<td>$x_{31}$</td>
<td>$x_{32}$</td>
<td>$x_{33}$</td>
</tr>
<tr>
<td>Daily abundance</td>
<td>$a_1$</td>
<td>$a_2$</td>
<td>$a_3$</td>
</tr>
<tr>
<td>Cumulative abundance</td>
<td>$A_1 = a_1$</td>
<td>$A_2 = A_1 + a_2$</td>
<td>$A_3 = A_2 + a_3$</td>
</tr>
<tr>
<td>Daily no. samples</td>
<td>$n_1$</td>
<td>$n_2$</td>
<td>$n_3$</td>
</tr>
</tbody>
</table>
Notation & definitions

\(x_{jt} = \) number of individuals in sample \(j\), day \(t\)

Data on day \(t\): \(\{x_{jt} | j = 1, \ldots, n_t\}, t = 1, \ldots\)

Daily samples on day \(t\): \(n_t\)

Daily abundance on day \(t\): \(a_t = \sum_{j=1}^{n_t} x_{jt}\)

**Cumulative** number of samples, abundance, mean, variance by day \(T\):

\[N_T = \sum_{t=1}^{T} n_t, \quad A_T = \sum_{t=1}^{T} a_t, \quad M_T = \frac{A_T}{N_T}\]

\[V_T = \text{var}\{x_{jt} | j = 1, \ldots, n_t, \ t = 1, \ldots, T\}\]

**Cumulative** precision by day \(T\):

\[C_T = \frac{\sqrt{V_T/N_T}}{M_T}\]
Cumulative precision & sample size

Cumulative precision by day $T$: $C_T = \sqrt{V_T / N_T}

Hence $C_T M_T = \sqrt{V_T / N_T}$, $(C_T M_T)^2 = V_T / N_T$,

$$N_T = V_T / (C_T M_T)^2.\]

For fixed $V_T, M_T$, increasing required precision from 50% to 10% increases required sample size by factor of 25.
Precision, sample size, & TL

When TL holds, $V_T = a(M_T)^b$ so $N_T = V_T/(C_T M_T)^2 = (a(M_T)^{b-2})/(C_T)^2$, so

$log N_T = log a + (b - 2) log M_T - 2 log C_T$.

Since $M_T = A_T/N_T$, we have (Green 1970),

$log A_T = log((C_T)^2/a) - \frac{b-1}{b-2} \log N_T$.

Slope of this "stopping line" is <0 if & only if $1 < b < 2$. Slope is >0 iff $b < 1$ or $b > 2$.

Stopping lines with positive or negative slopes & positive or negative intercepts exist in data.
Example: Lake Kariba fisheries, fished area (Xu, Kolding, Cohen 2019, CJFAS)
Example: Lake Kariba fisheries, fished area (Xu, Kolding, Cohen 2019, CJFAS)

Stopping lines were updated each day. Shown is first stopping line with $C = 0.1$ that intersected cumulative abundance plot.
Example: Lake Kariba fisheries, fished area
Xu, Kolding, Cohen 2019, Canadian J Fisheries & Aquatic Sciences
2019-09-10
When does stopping line intercept yield-effort curve?  
(Xu, Kolding, Cohen 2019, CJFAS)

From TL: \[ \log A_T = \frac{\log((c_T)^2/a)}{b-2} + \frac{b-1}{b-2} \log N_T \]

Empirical approximation to yield-effort curve: \[ \log A_T = L + K \log N_T, \ \& \ K < 1, = 1, > 1 \]

Stopping line intersects yield-effort curve iff

\( L < \frac{\log((c_T)^2/a)}{b-2} \) \ \& \ \( K > \frac{b-1}{b-2} \) \ \text{or} \\
\( L > \frac{\log((c_T)^2/a)}{b-2} \) \ \& \ \( K < \frac{b-1}{b-2} \).
This method could save work. In Lake Kariba data, using updated stopping lines of fixed precision 0.1 after each new sample, updated stopping-line method required 21% to 41% of the number of sampling days & 19% to 40% of number of samples that were planned a priori under systematic sampling, depending on sampling area (fished vs unfished) & abundance measure (number vs weight). Mean abundance estimates were similar to those from systematic sampling.


Tippett, Michael K. and Cohen, Joel E. 2016 Tornado outbreak variability follows Taylor’s power law of fluctuation scaling and increases dramatically with severity. Nature Communications 7:10668. DOI: 10.1038/ncomms10668

Merci!

Questions?
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