Matrix Population Models for Wildlife Conservation and Management

2-6 May 2022

Jean-Dominique LEBRETON, Jim HINES,
Xavier LAMBIN, Chris SUTHERLAND, Madan OLI

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Time-Varying and Random Environment Matrix Models

Shripad TULJAPURKAR ("Tulja") who extensively developed the theory of population models in random environment

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When the model matrix varies from year to year….

Time-Varying Models:
… in a known fashion over finite time window
- Recorded sequence of bad and poor years
- Relationship between demographic parameter and env. covariate
- MAIN AIM: model a known trajectory (retrospective)

Random Environment:
… in a random fashion over a finite or infinite time window
- Projection of relationship between parameter and env. covariate
- Unexplained year-to-year (environmental) variation
- MAIN AIM: projection, asymptotic behavior (prospective)

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Survival of storks in Baden-Württemberg estimated with rainfall in Sahel as a covariate

Model	Test	Parameters	AIC
(S_t,p_t)		31 parameters	1371.49
	$\chi^2_{14} = 7.70$, N.S.		
(S_t,p)		17 parameters	1349.50
	$\chi^2_{14} = 18.36$, N.S.		
(S_{rain},p)		3 parameters	**1339.15**
	$\chi^2_{1} = 18.96$, **** ; $\chi^2_{15} = 37.32$, **		
(S,p)		2 parameters	1356.10

Reducing the number of parameters results in
- *Higher precision*
- *Powerful tests of important biological hypotheses*

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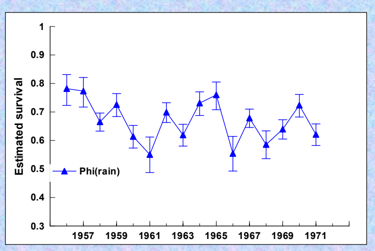
Survival of storks in Baden-Württemberg estimated with rainfall in Sahel as a covariate



Model	(S_t,p)	(S_{rain},p)	(S,p)
AIC	1349.50	**1339.15**	1356.10

$$\log (S / (1- S)) = a + b \text{ rain}$$

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Storks in Baden-Württemberg: Modelling numbers with survival driven by rainfall in Sahel

Year	57	58	...	i	i+1	...	74
Rain	x_{57}	x_{58}	...	x_i	x_{i+1}	...	x_{75}
Survival	ϕ_{57}	ϕ_{58}	...	ϕ_i	ϕ_{i+1}	...	ϕ_{75}
Matrix	M_{57}	M_{58}	...	M_i	M_{i+1}	...	M_{75}

Numbers obtained by a « time-varying matrix model » (using N_{56} based on average stable age structure):

$$N_{i+1}=M_i*N_i$$

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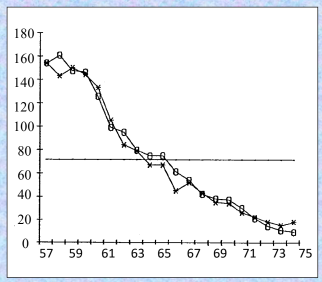
Storks in Baden-Württemberg: Modelling numbers with survival driven by rainfall in Sahel

An "ad hoc" comparison
(o = model)
(x =census)
based on
$a_3N_i(3)+N_i(4)$
(Nr of breeders)



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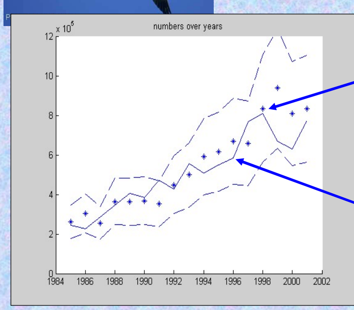
Likelihood based approach to time-varying models: State-space model

Greater snow goose



smoothed pop size
(dotted lines: 95 % CI)

Observed census

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Random Environment

the scalar exponential model
(no stage/age classes)

$n(t)=A_t\, n(t-1)$

A_t random scalar (i.i.d.) , with $E(A_t)=\lambda$

$E(n(t) / n(t-1)) = \lambda\, n(t-1)$

$E(n(t) / n(0)) \quad = \lambda^t\, n(0)$

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Random environment

Increasing variability

A_t = 1.15 with probability 1 $\Rightarrow \lambda$ = 1.15

A_t = 1.2 and 1.1 with prob. 0.5 $\Rightarrow \lambda$ = 1.15

A_t = 1.4 and 0.9 with prob. 0.5 $\Rightarrow \lambda$ = 1.15

A_t = 2.0 and 0.3 with prob. 0.5 $\Rightarrow \lambda$ = 1.15

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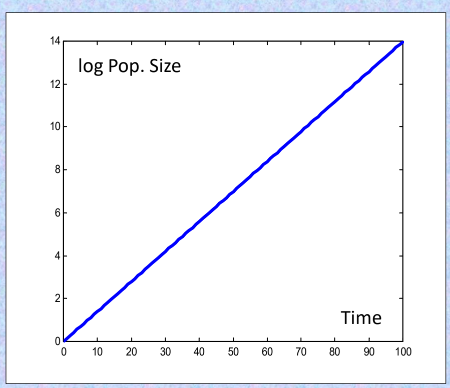
A_t = 1.15 with probability 1 $\Rightarrow \lambda$ = 1.15



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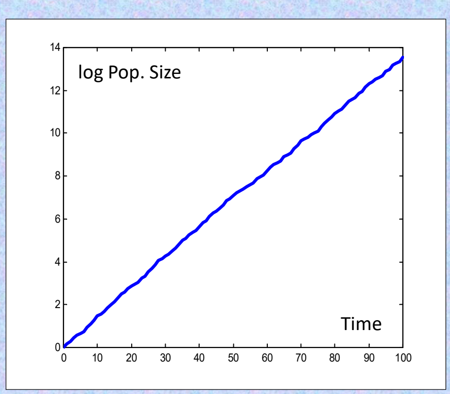
A_t = 1.2 and 1.1 with prob. 0.5 $\Rightarrow \lambda$ = 1.15



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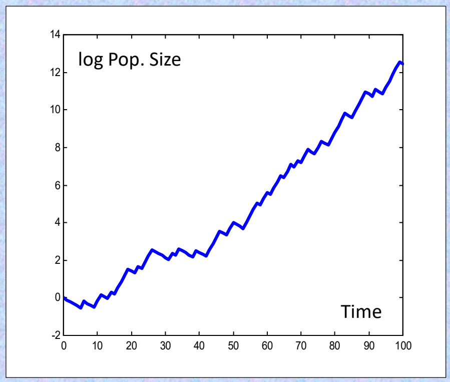

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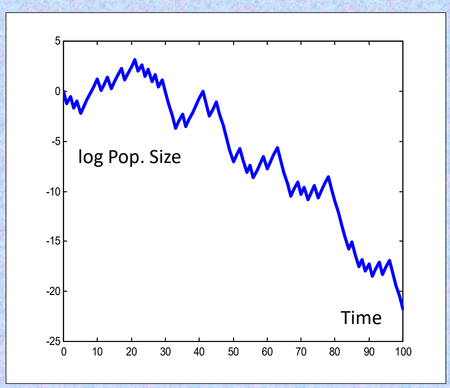
A_t = 2.0 and 0.3 with prob. 0.5 $\Rightarrow \lambda$ = 1.15



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Where is the paradox ?

$n(t) = A_t\, n(t-1) \Rightarrow n(t) = n(0)\, \Pi\, A_i$

$\log n(t) - \log n(0) = \Sigma \log A_i$

Central Limit Theorem: $\Sigma \log A_i \approx$ Normal distribution

$\log n(t) - \log n(0) \approx \textit{Normal}\,(\mu_t, \sigma^2_t)$

$a = E(\log A_t)$, $v = \mathrm{var}(\log A_t) \Rightarrow \mu_t = a\,t \quad \sigma^2_t = v\,t$

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The paradox is still there

$\log n(t) - \log n(0) \approx \textit{Normal}\ (\mu_t , \sigma^2_t)$

$\mu_t = a\,t\ ,\ \sigma^2_t = v\,t$

$\Rightarrow\ (\log n(t) - \log n(0))/t \approx \textit{Normal}\ (a , v/t)$

$1/t\ \ \log n(t) \approx \textit{Normal}\ (a , v/t)$

$v/t \to 0$ when $t \to \infty \Rightarrow$

$1/t\ \ \log n(t) \to \log \lambda_s = a = E(\log A_t)$

However $1/t\ \log E(n(t)) \to \log \lambda = \log E(A_t) = \mathrm{Log}(\lambda)$

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Is the paradox still there ?

A_t values	λ	EXPECTED $\log \lambda$	MOST PROBABLE $\log \lambda_s$
1.15	1.15	0.1398	0.1398
1.2 1.1	1.15	0.1398	0.1388
1.4 0.9	1.15	0.1398	0.1156
2.0 0.3	1.15	0.1398	-0.2554

Most probable and expected trajectories differ

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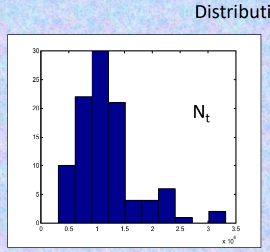
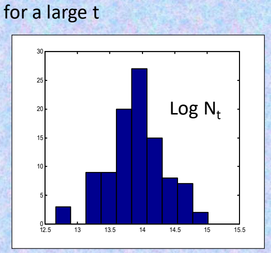
There is no real paradox

$n(t) \to$ log-normal distribution $\Rightarrow$ Median < Expectation

A_t = 1.2 and 1.1 with prob. 0.5

Distribution for a large t





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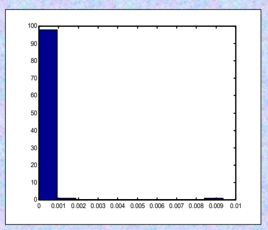
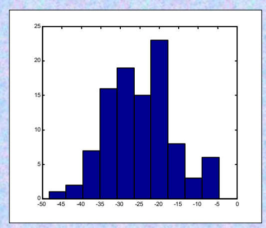
There is no real paradox

n(t) → log-normal distribution ⇒ Median < Expectation

A_t = 2.0 and 0.3 with prob. 0.5

Distribution for a large t





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There is no real paradox

A few trajectories with large growth rate keep the expected growth rate equal to $\log \lambda = \log E(A_t)$

Most probable trajectories are concentrated around $\log \lambda_s = E(\log A_t)$ (more and more when $t \to \infty$)

$\log \lambda_s$ is a relevant measure of growth rate

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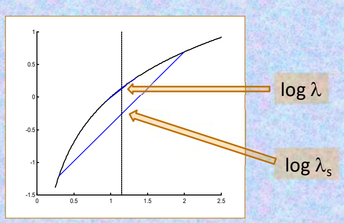
Environmental variability influences population growth

Jensen's inequality: $\log \lambda_s = E(\log A_t) \leq \log \lambda = \log E(A_t)$



Environmental variability depresses Population growth

A deterministically growing population may decrease

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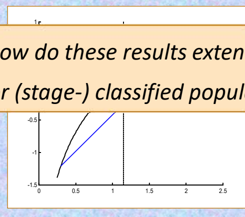
The effect of Environmental variability on Population growth



How do these results extend to age or (stage-) classified populations ?

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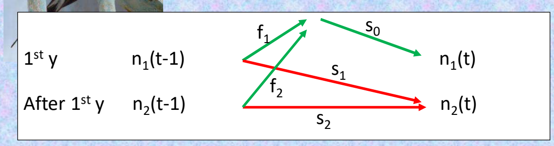
The Barn Swallow example



Average values
$s_0 = 0.2$ $f_1, f_2 = 3/2, 6/2$
$s_1 = 0.5$ $s_2 = 0.65$

$$A = \begin{pmatrix} f_1 s_0 & f_2 s_0 \\ s_1 & s_2 \end{pmatrix}$$

+ random Survival with variance σ^2

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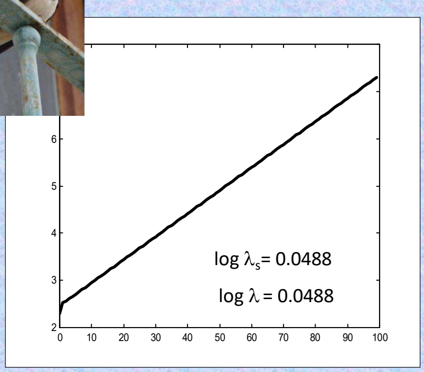
E(log N(t)), Constant Environment



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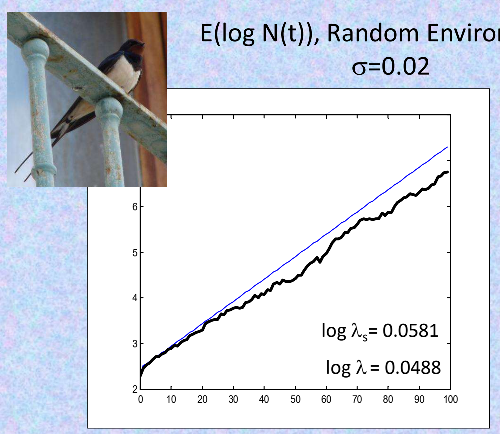
E(log N(t)), Random Environment
σ=0.02



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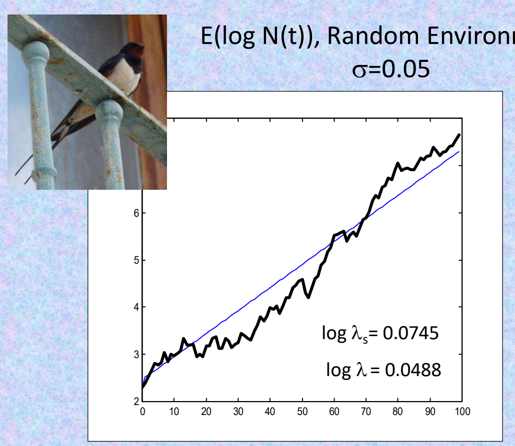
E(log N(t)), Random Environment
σ=0.05



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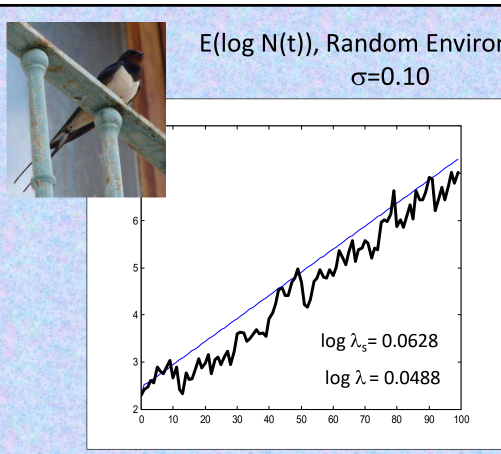
E(log N(t)), Random Environment
σ=0.10



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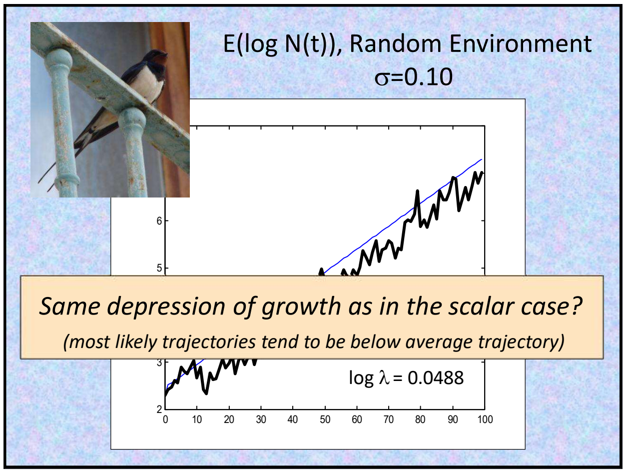
E(log N(t)), Random Environment
σ=0.10
Same depression of growth as in the scalar case?
(most likely trajectories tend to be below average trajectory)
log λ = 0.0488

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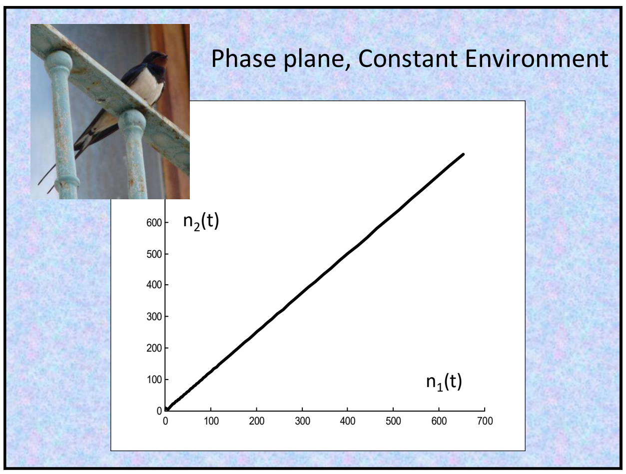
Phase plane, Constant Environment
n2(t)
n1(t)

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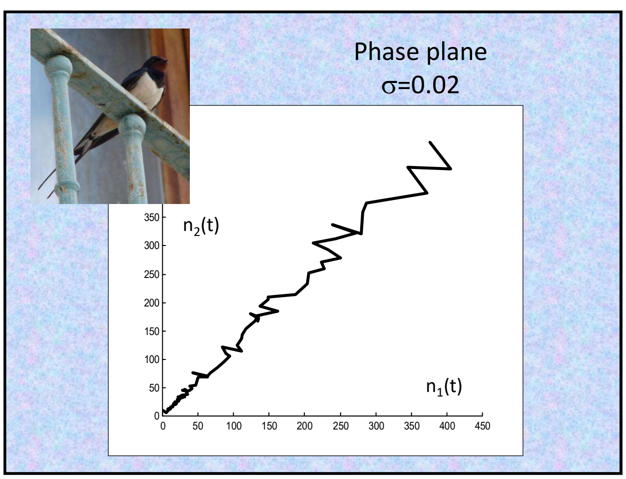
Phase plane
σ=0.02
n2(t)
n1(t)

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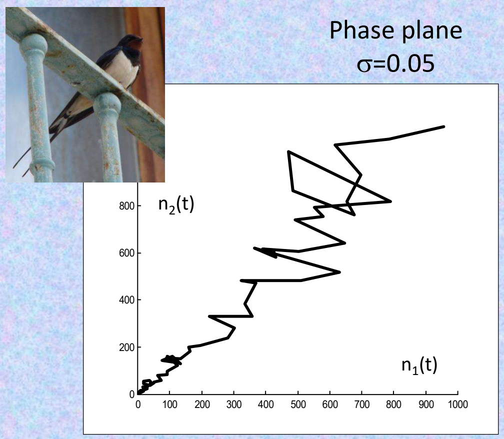
Phase plane
σ=0.05



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Same depression as above …plus a constant mismatch in age structure

$\log \lambda_s \neq \log(\lambda(E(A_t))) = \log \lambda$

$\log \lambda_s \neq E(\log(A_t))$, A_t being a matrix

$\log \lambda_s \neq \log E (\lambda(A_t))$, $n_t \neq$ eigenvector of A_t

Convergence of $1/t \log c' n(t)$ to $\log \lambda_s$
even under correlated environments
("*Ergodic theorems on products of random matrices*")

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How to calculate the asymptotic growth rate ?

"The computation is considerably more involved than in the scalar case"
S.Tuljapurkar (1990)

Simulation or Approximation

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Estimation of log λ_s
Simulation and approximation

- Simulation: R, Matlab, ULM...
  - Large number of repetitions needed
- Approximation : valid from small variability
  - For uncorrelated parameters:

$$\log \lambda_s \approx \log \lambda - \frac{1}{2\lambda^2} \Sigma \left(\frac{\partial \lambda}{\partial \theta}\right)^2 \mathrm{var}(\theta)$$

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Estimation of log λ_s
Approximation

σ	λ	log λ	APPROXIMATE log λ_s
0.00	1.05	0.0488	0.0488
0.01	1.05	0.0488	0.0486
0.05	1.05	0. 0488	0.0442
0.10	1.05	0.0488	0.0304

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