Stochastic fluctuations in population dynamics





Blue tit (Parus caeruleus)

Great tit (Parus maior)





Variation coefficient $CV = \sigma_N / N_{average}$ $\sigma_{\log N} \cong CV$ if CV < 30%





Swan (Cygnus olor)

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Extinction risk

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Chamois (*Rupicapra rupicapra*)







Soay sheep (*Ovis aries*)



CV of population fluctuations

CV = coefficient of variation = SD/Mean valueMakes sense for nonnegative variables like population size *N* For CV < 30% CV \simeq SD(log*N*)

Table 1.1 Coefficient of variation (CV) for fluctuations in annual population size in birds. CV is calculated only for the last 20 years of data. α = average age at first breeding of females

Species		α	Locality	Period	CV	Reference
Blue Tit	Parus caeruleus	1	Lower Saxony, Germany	1974–93	0.27	Winkel (1996)
Dipper	Cinclus cinclus	1	Lygnavassdraget, southern Norway	1978-97	0.46	Sæther et al. (2000b)
Garganey	Anas querquedula	1	Engure Marsh, Latvia	1974-93	0.48	Blums et al. (1993)
Great Tit	Parus major	1	Lower Saxony, Germany	1974-93	0.17	Winkel (1996)
Great Tit	Parus major	1	Wytham Wood, Oxford, England	1974-93	0.27	McCleery (pers. com.)
Northern Shoveler	Anas clypeata	1	Engure Marsh, Latvia	1974-93	0.38	Blums et al. (1993)
Nuthatch	Sitta europaea	1	Lower Saxony, Germany	1974-93	0.31	Winkel (1996)
Pied Flycatcher	Ficedula hypoleuca	1	Lower Saxony, Germany	1974-93	0.22	Winkel (1996)
Pied Flycatcher	Ficedula hypoleuca	1	Lingen, Germany	1974-93	0.25	Winkel (1998)
Pied Flycatcher	Ficedula hypoleuca	1	Kilpisjärvi, northern Finland	1968-87	0.45	Järvinen (1990)
Pochard	Aythya ferina	1	Engure Marsh, Latvia	1974-93	0.51	Blums et al. (1993)
Seychelles Warbler	Acrocephalus sechellensis	1	Cousin Island, Seychelles	1973–93 ¹	0.10	Komdeur (1994)
Song Sparrow	Melospiza melodia	1	Mandarte Island, British Columbia, Canada	1979-98	0.49	Sæther et al. (2000a)
Tufted Duck	Aythya fuligula	1	Engure Marsh, Latvia	1974-93	0.25	Blums et al. (1993)
Avocet	Recurvirostra avosetta	2	Havergate, Suffolk, England	1967-86	0.30	Hill (1988)
Grey Heron	Ardea cinera	2	Southern England	1979-98	0.09	B.T.O. (pers. com.)
Kentish Plover	Charadrius alexandrinus	2	Niedersachsen, Germany	1974-93	0.57	Hälterlein and Südbeck (1996)
Ural Owl	Strix uralensis	2	Hämeenlinna, Finland	1969-88	0.50	Saurola (1989)
Common Tern	Sterna hirundo	3	Mecklenburg-Vorpommern, Germany	1978-97	0.39	Spretke (1998)
Sandwich Tern	Sterna sandvicensis	3	Schleswig-Holstein, Germany	1974-93	0.44	Hälterlein and Südbeck (1996)
Mute Swan	Cygnus olor	4	River Thames, England	1920-39	0.15	Cramp (1972)
South Polar Skua	Catharacta maccormicki	6	Pointe Géologie, Terre Adélie, Antarctica	1981-2000	0.19	Weimerskirch (pers. com.)
Short-tailed Shearwater	Puffinus tenuirostris	7	Fisher Island, Tasmania	1965-84	0.15	Bradley et al. (1991)
Northern Fulmar	Fulmarus glacialis	9	Eynhallow, Orkney	1958-77	0.27	Dunnet et al. (1979)
Wandering Albatross	Diomedea exulans	10	Bird Island, South Georgia	1974-93	0.06	Croxall et al. (1997)

¹ Only 15 censuses available during the last 20 study years.



Deterministic and stochastic components

Fluctuations in population dynamics can be due to

- Deterministic drivers:
 - High fertility;
 - Seasonality;
 - Interactions (predation ...)
- Stochastic drivers:
 - demographic (Bighorn sheep)
 - environmental (Flamingoes in South Africa);

 $N_{t+1} = \lambda_t N_t$



Examples





Bighorn sheep (Ovis canadensis)

Surviving populations (%)





Examples

Circles indicate reproduction success



Flamingo (*Phoenicopterus ruber*)



Phoeniconaias minor



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Extinctions: deterministic or stochastic?





(Parr, 1992), the Wild Dog Lycaon pictus in Serengeti National Park, Tanzania (Burrows et al., 1995), two populations of House Sparrow Passer domesticus at Helgeland, northern Norway

1991).







Extinction risk

Discrete-time demography

 $N_{t+1} = \lambda_t N_t$

Individual fitness Contribution of individual *i* at time *t* to next generation *t* + 1

$$w_{i,t} \implies N_{t+1} = \sum_{i=1}^{N_t} w_{i,t}$$
Is there a relationship?

N.B. Better if you always think that N_t is the number of females



Calculating fitnesses

Problem ER10

In 2023 a population of pink finches in the natural reserve of Greybeeches consists of only three adult reproductive females (from now on called A, B, C). They breed in mid spring. You know that:

- Female A produces 7 eggs, of which only 5 hatch; 3 nestlings are female and of them 2 will survive till adulthood and will reproduce in 2024; female A dies in December 2023;
- Female B produces 4 eggs, all of which hatch; 1 nestling is female but will not survive till adulthood; female B is still alive in mid spring 2024;
- Female C produces 9 eggs, of which only 6 hatch; 4 nestlings are female and of them 3 will survive till adulthood and will reproduce in 2024; female C is still alive in mid spring 2024;

Calculate the individual fitnesses of A, B e C and the finite rate of increase of the population between 2023 and 2024.

Female A:2+0 fitness(A)=2; fitness(B)=0+1=1; fitness(C)=3+1=4 N(2024)=2+1+4=7 N(2023)=3 λ_2 2023=N(2024)/N(2023)=7/3=2.333



Environmental vs. demographic stochasticity

$$N_{t+1} = \lambda_t N_t = \sum_{i=1}^{N_t} w_{i,t} \qquad \lambda_t = \sum_{i=1}^{N_t} \frac{W_{i,t}}{N_t}$$



 $W_{i,t} = \overline{W}_t + \delta_i$ $E\left[\delta_{i}\right] = 0$ $Var\left[\delta_{i}\right] = \sigma_{d}^{2}$ $\begin{cases} E\left[\overline{w}_{t}\right] = w \\ Var\left[\overline{w}_{t}\right] = \sigma_{e}^{2} \end{cases}$ $\begin{bmatrix} E \begin{bmatrix} \lambda_t | N_t = N \end{bmatrix} = ?$ $Var \begin{bmatrix} \lambda_t | N_t = N \end{bmatrix} = ?$

where

Extinction risk



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Environmental vs. demographic stochasticity

$$N_{t+1} = \lambda_t N = \sum_{i=1}^{N_t} w_{i,t}$$

$$\lambda_{t} = \sum_{i=1}^{N} \frac{w_{i,t}}{N} = \sum_{i=1}^{N} \frac{w_{t} + \delta_{i}}{N} = w_{t} + \sum_{i=1}^{N} \frac{\delta_{i}}{N}$$
$$E[\lambda_{t}] = w$$
$$Var[\lambda_{t}] = Var[w_{t}] + \frac{Var[\sum_{i=1}^{N} \delta_{i}]}{N^{2}} = \sigma_{e}^{2} + \sigma_{d}^{2}/N$$

Typical values of σ_{e}^{2} and σ_{d}^{2}

$$N \gg \frac{\sigma_d^2}{\sigma_e^2}$$

e.g. $N = 10 \frac{\sigma_d^2}{\sigma_e^2} = N$

С

2

Table 1.2 Estimated demographic variance, $\hat{\sigma}_d^2$, and environmental variance, $\hat{\sigma}_e^2$, in multiplicative growth rate in populations with different mean age at first breeding of females, α

Species	Locality	α	$\hat{\sigma}_d^2$	$\hat{\sigma}_e^2$	Reference
Barn Swallow, Hirundo rustica	Denmark	1	0.18	0.024	Engen <i>et al</i> . (2001)
Dipper	Southern Norway	1	0.27	0.21	Sæther <i>et al.</i> (2000 <i>b</i>)
Great Tit	Wytham Wood, U.K.	1	0.57	0.079	Sæther <i>et al.</i> (1998 <i>a</i>)
Pied Flycatcher	Hoge Veluwe, Netherlands	1	0.33	0.036	Sæther <i>et al.</i> $(2002a)$
Song Sparrow	Mandarte Island, B.C.	1	0.66	0.41	Sæther <i>et al.</i> $(2000a)$
Soay Sheep, Ovis aries	Hirta Island, U.K.	1	0.28	0.045	Sæther et al. (unpubl.)
Brown Bear, Ursus arctos	Southern Sweden	4	0.16	0.003	Sæther <i>et al.</i> (1998 <i>b</i>)
Brown Bear	Northern Sweden	5	0.18	0.000	Sæther <i>et al</i> . (1998 <i>b</i>)

Calculate critical population

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Extinction risk

Demographic stochasticity

•We use a continuous time model (birth-death process)

•Poisson assumption: in a very short time *dt* at most one event can occur: nothing, one birth, one death

•Malthusian case

- Variables $p_i(t)$ = probability that population contains *i* individuals at time *t*
- Demographic parameters (birth rate ν and mortality rate μ are constant)

- v dt = probability a mother produces one birth (daughter) between t and t+dt

- μdt = probability one mother dies between *t* and *t*+*dt*
- 1 v dt μdt = probability no event
- so-called Kolmogorov equations describe dynamics of $p_i(t)$
- *N*(*t*) is a stochastic variable at any time *t* (stochastic process)

Important property of the expected value of N(t) at any time t

$$\overline{N}(t) = E\left[N(t)\right] = \sum_{i=0}^{\infty} ip_i(t) \qquad \Rightarrow \quad \frac{d\overline{N}(t)}{dt} = \left(v - \mu\right) \quad \overline{N}(t)$$



Realizations of birth-death stochastic process

$$\overline{N}(t) = N(0) \exp(rt)$$
 $r = v - \mu$



Variance of total number increases with time **There can be extinctions!**



The extinction risk

 $p_0(t)$ = probability that population contains 0 individuals at time t = probability of extinction = probability that time of extinction is $\leq t$

$$p_0(t) = \left(\frac{\mu \exp(rt) - \mu}{\nu \exp(rt) - \mu}\right)^{N_0} \implies \begin{cases} \text{if } r < 0, \quad \lim_{t \to \infty} p_0(t) = \cdots \\ \text{if } r = 0, \quad \lim_{t \to \infty} p_0(t) = \cdots \\ \text{if } r > 0, \quad \lim_{t \to \infty} p_0(t) = \cdots \end{cases}$$

$$N_0$$
 = number of
reproductive
females

Long-term risk

$$\begin{split} \lim_{t \to \infty} p_0(t) &= \left(\frac{-\mu}{-\mu}\right)^{N_0} = 1. \qquad r < 0 \\ \lim_{t \to \infty} p_0(t) &= \lim_{t \to \infty} \left(\frac{\mu \exp(rt) - \mu}{\nu \exp(rt) - \mu}\right)^{N_0} = \left(\frac{\mu}{\nu}\right)^{N_0} = \left(\frac{\mu}{r + \mu}\right)^{N_0}. \quad r > 0 \\ \lim_{r \to 0} p_0(t) &= \lim_{r \to 0} \left(\frac{\mu t \exp(rt)}{(\mu + r)t \exp(rt) + \exp(rt)}\right)^{N_0} = \left(\frac{\mu t}{1 + \mu t}\right)^{N_0}. \end{split}$$

Extinction risk

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Extinction probability (demographic stochasticity)

				1	
N_0	Asymptotic				
	Extinct. Prob.	Extinct. 10	Extinct. 50		
1	0.909090909	0.8634105	0.908531	Probability of asymptotic	
5	0.620921323	0.4798291	0.61901	extinction and after 10 and	
10	0.385543289	0.2302359	0.383174	50 generations	
50	0.008518551	0.0006469	0.00826	$r = 0.05$ and $\mu = 0.5$ time ⁻¹	ν
100	7.25657E-05	4.185E-07	6.82E-05	generation time = $1/\mu$	
500	2.01214E-21	1.284E-32	1.48E-21		

v = 0.55

N	$t_0 = t = 1/\mu$	$t = 10/\mu$	<i>t</i> =100/μ	<i>t</i> =1000/μ	
	1 0.5	0.909	0.990	0.999	Extinction
	5 0.031	0.621	0.951	0.995	probability in
10	0.00097	7 0.386	0.905	0.990	stationary
50	0 8.88 10	⁻⁶ 0.0085	0.608	0.951	populations $(r = 0)$
100	0 7.89 1	0 0.000072	0.370	0.905	for varying N_0 at
	31				different
500	0~0	2.01 10 ⁻²¹	0.0069	0.607	generations

Average and median extinction time (hint: $p_0(t)$ is a cdf)



Demographic stochasticity and densitydependence

In nonMalthusian case

Extinction is certain in the long term, however ...

$$\lim_{t\to\infty}p_0(t)=1$$



Extinction risk

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Environmental stochasticity

$$N_{t+1} = \sum_{i=1}^{N_t} w_{i,t} = \overline{w}_t N_t = \lambda_t N_t$$

where

$$\lambda_t = \delta_t \Lambda(N_t) = \exp(\varepsilon_t) \Lambda(N_t)$$

White noise

$$\begin{cases} E\left[\varepsilon_{t}\right]=0\\ E\left[\varepsilon_{t}^{2}\right]=Var\left[\varepsilon_{t}\right]=\sigma_{\varepsilon}^{2}\\ E\left[\varepsilon_{t}\varepsilon_{t-\tau}\right]=0 \end{cases}$$



Environmental stochasticity: the Malthusian case

$$\begin{split} \lambda_{t} &= \delta_{t} \Lambda \left(N_{t} \right) = \exp \left(\varepsilon_{t} \right) \lambda \qquad \lambda = \text{median!} \\ \text{where} \qquad N_{t} &= \lambda_{t-1} \lambda_{t-2} \cdots \lambda_{0} N_{0} = \lambda^{t} \exp \left(\varepsilon_{t-1} + \varepsilon_{t-2} + \cdots + \varepsilon_{0} \right) N_{0} \\ \text{Take logarithms} \\ \log \left(N_{t} \right) &= t \log(\lambda) + \log \left(N_{0} \right) + \sum_{i=0}^{t-1} \varepsilon_{i} \\ \log \left(N_{t} \right) &= t \log(\lambda) + \log \left(N_{0} \right) + \sum_{i=0}^{t-1} \varepsilon_{i} \\ \text{Var} \left[\sum_{i=0}^{t-1} \varepsilon_{i} \right] &= \sum_{i=0}^{t-1} Var \left[\varepsilon_{i} \right] = t \sigma_{\varepsilon}^{2} \end{split}$$

Result: log(*N*_t) is distributed as a Normal with

$$\begin{cases} E\left[\log\left(N_{t}\right)\right] = t\log\left(\lambda\right) + \log\left(N_{0}\right) + \sum_{i=0}^{t-1} E\left[\varepsilon_{i}\right] = rt + \log\left(N_{0}\right) \\ Var\left[\log\left(N_{t}\right)\right] = E\left[\left(\log\left(N_{t}\right) - E\left[\log\left(N_{t}\right)\right]\right)^{2}\right] = E\left[\sum_{i=0}^{t-1} \varepsilon_{i}^{2}\right] = \sum_{i=0}^{t-1} Var\left[\varepsilon_{i}\right] = t\sigma_{\varepsilon}^{2} \end{cases}$$

Environmental stochasticity: the Malthusian case





Environmental stochasticity: the Malthusian case

$\log(\lambda) = r > 0$

then population increases.

Remark: logarithm of median must be positive not logarithm of average!

In fact, with lognormal noise

$$E[\lambda_t] = E[\lambda\delta_t] = \lambda E[\delta_t] = \lambda \exp\left(\frac{\sigma_{\varepsilon}^2}{2}\right) > \lambda$$

Therefore, using the average of λ_t 's can be misleading and produce an overestimation of the population growth rate

Example

If

Annual population with finite rate of increase equal to 1.1 in normal years and 0.3 in critical years that occur once in a decade. What is the fate of the population?







Extinction risk and environmental stochasticity

Whenever environmental stochasticity brings population below a critical threshold it can be captured by an extinction "vortex":

 $N < N_c \implies$ quasiextinction

How to estimate quasiextinction probability? Based on *r* and σ^2_{ϵ} ...



How to estimate σ_{ε}^{2} ? $\log(N_{t+1}/N_{t}) = r + \varepsilon_{t}$

Use estimate of r

$$\hat{\varepsilon}_{t} = \log(N_{t+1}/N_{t}) - \hat{r}$$
$$\hat{\sigma}_{\varepsilon}^{2} = \frac{1}{m-2} \sum_{i=1}^{m-1} \hat{\varepsilon}_{i}^{2}$$



Normal distribution table

 $Prob{N_t < N_c} = Prob{InN_t < InN_c} =$ Introduce standard Normal



 $Prob\{InN_t < InN_c\} = Prob\{standard normal < Z_c\}$





-										
.0	.5000	.5040	.5080	.5120	.5160	.5199	.5239	.5279	.5319	.5359
.1	.5398	.5438	.5478	.5517	.5557	.5596	.5636	.5675	.5714	.5753
.2	.5793	.5832	.5871	.5910	.5948	.5987	.6026	.6064	.6103	.6141
.3	.6179	.6217	.6255	.6293	.6331	.6368	.6406	.6443	.6480	.6517
.4	.6554	.6591	.6628	.6664	.6700	.6736	.6772	.6808	.6844	.6879
.5	.6915	.6950	.6985	.7019	.7054	.7088	.7123	.7157	.7190	.7224
.6	.7257	.7291	.7324	.7357	.7389	.7422	.7454	.7486	.7517	.7549
.7	.7580	.7611	.7642	.7673	.7704	.7734	.7764	.7794	.7823	.7852
.8	.7881	.7910	.7939	.7967	.7995	.8023	.8051	.8078	.8106	.8133
.9	.8159	.8186	.8212	.8238	.8264	.8289	.8315	.8340	.8365	.8389
1.0	.8413	.8438	.8461	.8485	.8508	.8531	.8554	.8577	.8599	.8621
1.1	.8643	.8665	.8686	.8708	.8729	.8749	.8770	.8790	.8810	.8830
1.2	.8849	.8869	.8888	.8907	.8925	.8944	.8962	.8980	.8997	.9015
1.3	.9032	.9049	.9066	.9082	.9099	.9115	.9131	.9147	.9162	.9177
1.4	.9192	.9207	.9222	.9236	.9251	.9265	.9279	.9292	.9306	.9319
1.5	.9332	.9345	.9357	.9370	.9382	.9394	.9406	.9418	.9429	.9441
1.6	.9452	.9463	.9474	.9484	.9495	.9505	.9515	.9525	.9535	.9545
1.7	.9554	.9564	.9573	.9582	.9591	.9599	.9608	.9616	.9625	.9633
1.8	.9641	.9649	.9656	.9664	.9671	.9678	.9686	.9693	.9699	.9706
1.9	.9713	.9719	.9726	.9732	.9738	.9744	.9750	.9756	.9761	.9767
2.0	.9772	.9778	.9783	.9788	.9793	.9798	.9803	.9808	.9812	.9817
2.1	.9821	.9826	.9830	.9834	.9838	.9842	.9846	.9850	.9854	.9857
2.2	.9861	.9864	.9868	.9871	.9875	.9878	.9881	.9884	.9887	.9890
2.3	.9893	.9896	.9898	.9901	.9904	.9906	.9909	.9911	.9913	.9916
2.4	.9918	.9920	.9922	.9925	.9927	.9929	.9931	.9932	.9934	.9936
2.5	.9938	.9940	.9941	.9943	.9945	.9946	.9948	.9949	.9951	.9952
2.6	.9953	.9955	.9956	.9957	.9959	.9960	.9961	.9962	.9963	.9964
2.7	.9965	.9966	.9967	.9968	.9969	.9970	.9971	.9972	.9973	.9974
2.8	.9974	.9975	.9976	.9977	.9977	.9978	.9979	.9979	.9980	.9981
2.9	.9981	.9982	.9982	.9983	.9984	.9984	.9985	.9985	.9986	.9986
3.0	.9987	.9987	.9987	.9988	.9988	.9989	.9989	.9989	.9990	.9990

Environmental stochasticity and density dependence





Stochastic Ricker model $N_{t} = \lambda N_{t} exp(-\beta N_{t} + \epsilon_{t})$ $\ln\left(\frac{N_{t+1}}{N_{t}}\right) = \log \lambda - \beta N_{t} + \epsilon_{t}$

Red Deer abundance in Yellowstone Park, and logarithmic rate of increase vs deer abundane (data and linear regression)

Marino Gatto and Renato Casagrandi



Environmental stochasticity and density dependence



- extinction probability vs time;
- average and median extinction time

Extinction vortices





Population Viability Analysis (PVA)





African elephants

Software: VORTEX, RAMAS, ALEX ...

http://www.ramas.com

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Equal risk curves

Mace and Lande's Criteria for Threatened Species (1991)

How to classify threatened species

Risk=Decline × ProbDecline

	Population Trait	Critical	Endangered	Vulnerable
A	Observed decline	80% in 10 years or 3 generations	50% in 10 years or 3 generations	20% in 10 years or 3 generations
B	Geographical range	< 100 km ² single location	$< 5000 \text{ km}^2$ < 5 locations	< 20,000 km ² < 10 locations
С	Total population	$\begin{array}{l} N < 250 \\ N_s < 50 \end{array}$	N < 2,500 $N_s < 250$	N < 10,000 $N_s < 1000$
D	Projected decline	> 25% in 3 years or 1 generation	> 20% in 5 years or 2 generations	>20% in 10 years or 3 generations
E	Extinction probability	> 50% in 10 years or 3 generations	>20% in 20 years or 5 generations	>10% in 100 years

Note: N, refers to the sizes of subpopulations that are found in different parts of the total range occupied by the species.

IUCN (International Union for Conservation of Nature) classification: Mace and Lande slightly modified



Ex. Category CR

- Criterion D: Population size of mature individuals N < 50
- Criterion E: Extinct. Probab. ≥ 50% within next 10 years or next 3 generations

http://www.iucn.org/

https://www.iucnredlist.org/

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Tabella 1. Categorie di minaccia delle piante vascolari italiane valutate secondo i criteri IUCN
(2001).

Categoria <i>Red List</i> IUCN	Policy species	Non Policy species	Totale
Estinta (EX)	0	2	2
Estinta a livello regionale (RE)	1	0	1
Estinta in Natura (EW)	0	1	1
Probabilmente Estinta CR (PE)	7	4	11
Probabilmente Estinta in natura CR (PEW)	0	1	1
Gravemente minacciata (CR)	18	78	96
Minacciata (EN)	35	41	76
Vulnerabile (VU)	10	12	22
Quasi Minacciata (NT)	24	7	31
A Minor Rischio (LC)	40	0	40

Endangered vascular plants in Italy

Tabella 4. Categorie di minaccia dei vertebrati italiani

Categoria Red List IUCN	Specie terrestri	Specie marine
Estinto nella regione (RE)	6	0
In Pericolo Critico (CR)	17	12
In Pericolo (EN)	42	7
Vulnerabile (VU)	79	4
Quasi minacciata (NT)	50	3
Minor Preoccupazione (LC)	254	17
Dati Insufficienti (DD)	27	38
Non Applicabile (NA)	101	15
Totale	576	96

Endangered vertebrates in Italy

