INTERNATIONAL ATOMIC ENERGY AGENCY
UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION
INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
I.C.T.P., P.O. BOX 586, 34100 TRIESTE, ITALY, CABLE: CENTRATOM TRIESTE

UNITED NATIONS INDUSTRIAL DEVELOPMENT ORGANIZATION
INTERNATIONAL CENTRE FOR SCIENCE AND HIGH TECHNOLOGY
c/o INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS 34100 TRIESTE (ITALY) VIA GRIGNANO, 9 (ADRIATICO PALACE) P.O. BOX 586 TELEPHONE 040-224572 TELEFAX 040-224575 TELEX 460449 APH I

SMR.648 - 11

SECOND AUTUMN WORKSHOP ON MATHEMATICAL ECOLOGY

(2 - 20 November 1992)

"Risk Assessment in Conservation Biology"

H. Resit Akcakaya
Applied Biomathematics
100 North Country Road
Setauket, New York 11733
U.S.A.

These are preliminary lecture notes, intended only for distribution to participants.

Risk Assessment in Conservation Biology

H. Reşit Akçakaya
Applied Biomathematics
Setauket, New York, USA

Risk assessment measures in conservation biology

Language of risk analysis

Time to extinction

Risk of extinction

Risk of decline

Recovery chance

Risk assessment models in conservation biology

Scalar (unstructured)

Age-structured (chronological) and Stage-structured (physiological, morphological)

Spatially structured (metapopulation models)

Issues in Conservation

Assessing the viability of species and populations

e.g. What is the chance of recovery of species X to level A?
What is the risk of extinction of species X in the next 50 years?

Wildlife Management

e.g. Is it better to prohibit hunting or to protect more habitat for population X?

Which harvesting strategy maximizes harvest and minimizes risk of decline?

Captive breeding

e.g. Is captive breeding and reintroduction to natural habitat patches a viable strategy for conserving species X?

Reintroduction

e.g. Is it better to reintroduce 100 individuals of species X to patch A or 50 individuals each to patches A and B?

Translocation

e.g Which schedule of translocating individuals among patches has the greatest effect on viability of species X?

Reserve Design

e.g. Is it better to preserve forest fragment A, or B or C+D to protect species X? (Single large vs. several small; close vs. distant)

Is it better to add another patch to the reserve system, or enhance habitat corridors to increase dispersal among existing patches?

Population viability analysis

identification of factors (natural factors, human impact, and conservation and management options)

determination of the model structure to use

estimation of population parameters (field observations and experiments)

statistical analyses of the data

risk analysis: combining the existing information into predictions about the persistence of species

implementation of conservation options, long-term monitoring and evaluation.

Language of risk analysis

Extinction time

Mean extinction time

Median extinction time

Distribution of extinction times

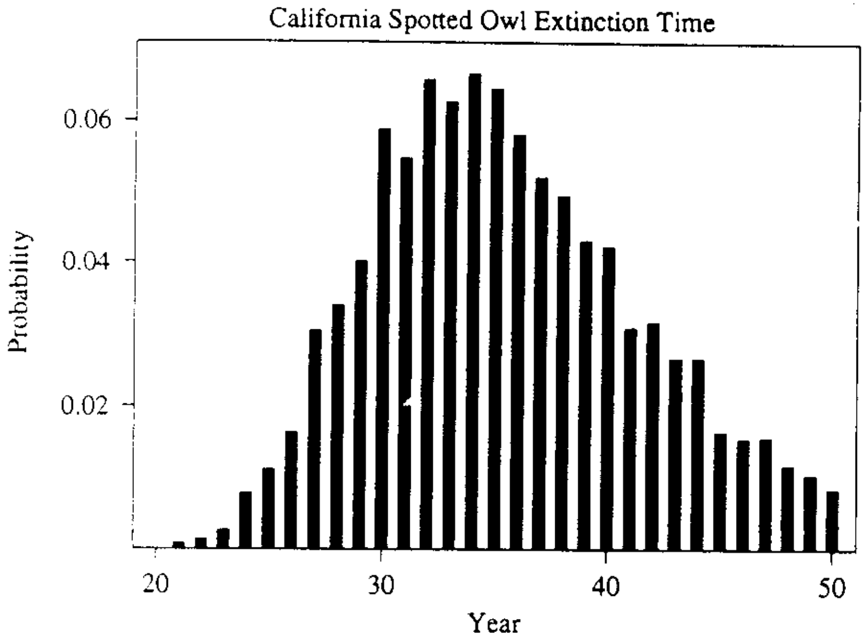


Figure 1 . Extinction time, i.e., the predicted distribution of the number of years that will pass before the spotted owl population goes extinct. Each vertical bar shows the probability of extinction at a particular year.

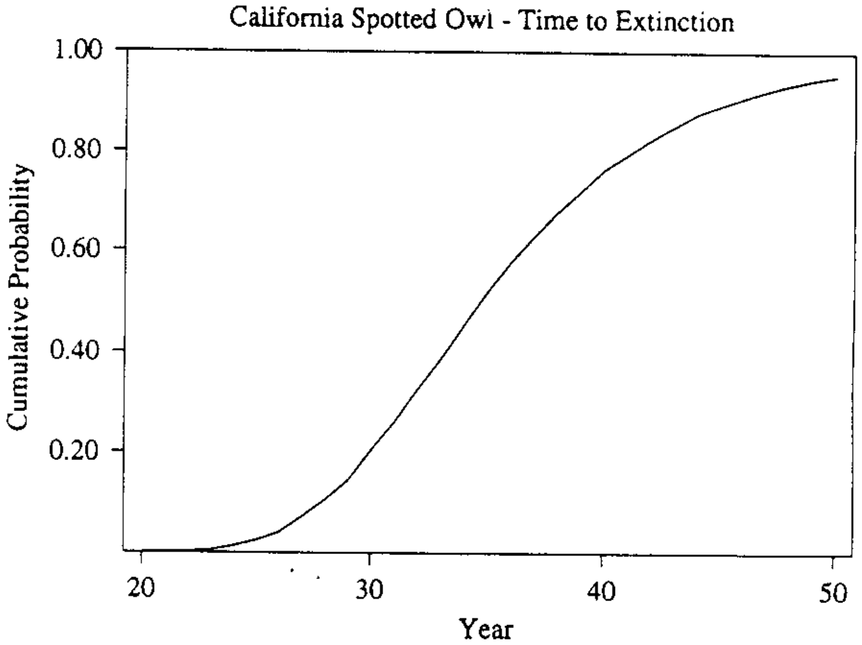


Figure 2 . Cumulative time to extinction, i.e., the number of years that will pass before the spotted owl population goes extinct.

Quasi-extinction time

Partial decline or loss

Useful for wildlife management in addition to conservation.

Threshold, especially for economically important species or a biologically critical level of abundance.

Difficulty of predicting the behavior of small populations
    Allee effects
    Inbreeding depression

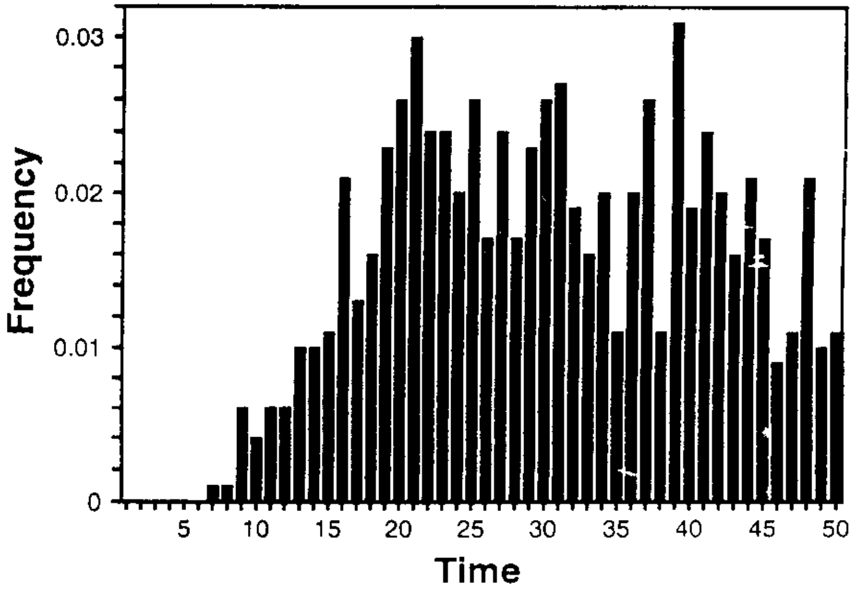


Figure 3 . Quasi-extinction time, i.e., the predicted distribution of the number of years that will pass before the bear population falls to 20 individuals starting from an initial size of about 80.

Risk

Extinction risk

Quasiextinction risk

Risk of decline

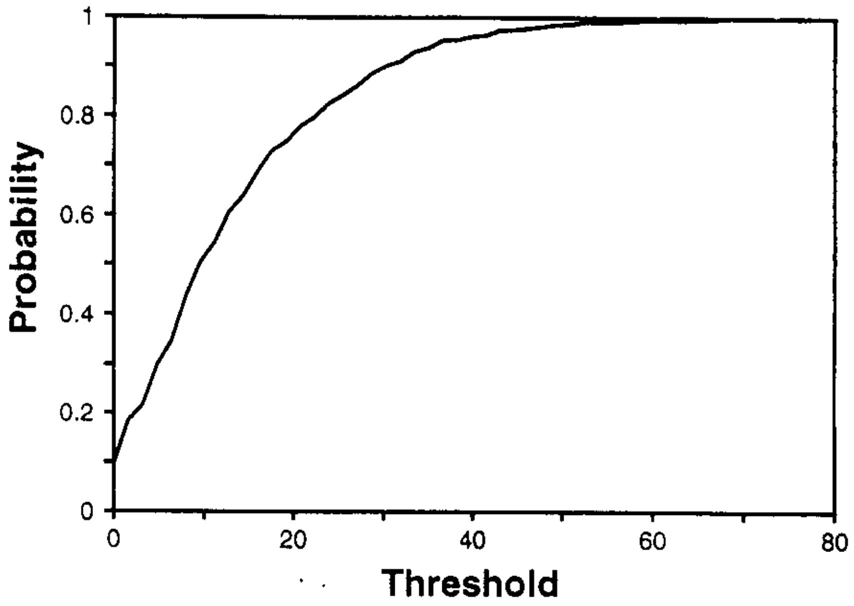


Figure 4 . Quasi-extinction risk, i.e., the predicted risks of the total population of grizzly bears falling lower than a threshold population size in the next 50 years.

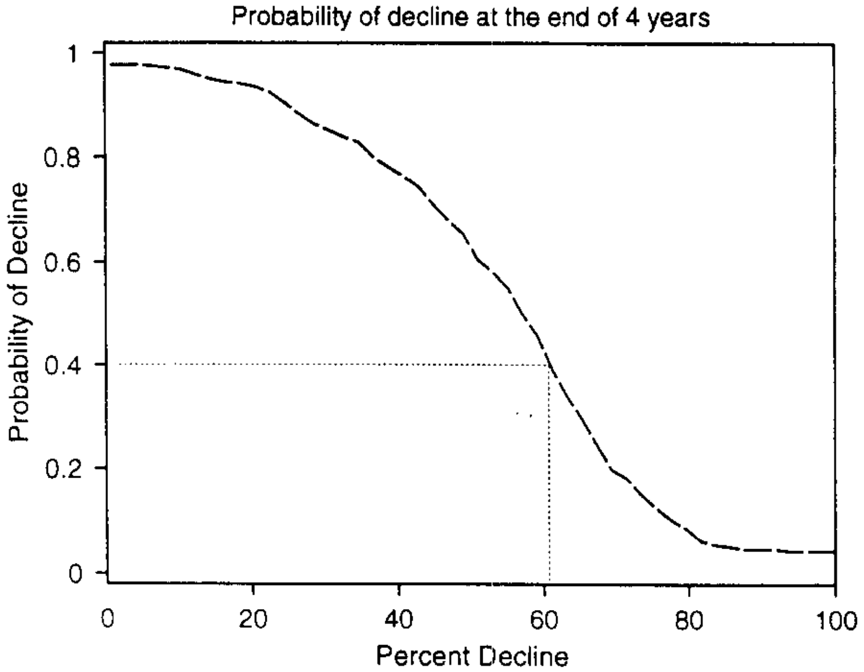


Figure 5 . Probability of decline as a function of the magnitude of decline.

Recovery

Recovery time

Recovery chance

Quasi-explosion Risk

Summary of PVA Measures

Decline/ growth	*Threshold*	*Time*	*Prob.*	*Measure*
↓	fixed at 0	?	?	Extinction time
↓	fixed at 0	specified	?	Extinction risk
↓	specified	?	?	Quasi-extinction time
↓	?	specified	?	Quasi-extinction or decline risk
↑	fixed	?	?	Explosion time
↑	fixed	specified	?	Explosion risk
↑	specified	?	?	Quasi-explosion time
↑	?	specified	?	Quasi-explosion risk
↑	defined	?	?	Recovery time
↑	defined	specified	?	Recovery chance

Models for Population Viability Analysis

Time

Discrete-time models (difference equations)

$$N(t+1) \;=\; f\;[\;N(t)\;]$$

Continuous-time models (differential equations)

$$\frac{dN}{dt} \;=\; f\;[\;N\;]$$

Solution

Analytical (stability analysis)

Numerical (simulations)

Variation

Deterministic: $N(t+1) \;=\; f\;[\;N(t)\,,\,p\;]$

Stochastic: $N(t+1) \;=\; f\;[\;N(t)\,,\,p(t)\;]$

Structure

Scalar (unstructured)

Age-structured (chronological)

Stage-structured (physiological, morphological)
    size or weight classes; egg, larva, pupae, adult
    juvenile, non-breeding adult, breeding adult

Spatially structured (metapopulations)

Scalar (unstructured) models

Single number to describe the population: population size, N

Exponential growth (no density dependence):

Continuous-time:

$$\frac{dN}{dt} = f\,[\,N\,]$$

$$\frac{dN}{dt} = r\;N$$

r is the instantaneous rate of increase:

$r < 0$ declining N,

$r = 0$ unchanging N,

$r > 0$ increasing N.

Discrete-time:

$$N(t+1) = f\,[\,N(t)\,]$$

$$N(t+1) = R\;N(t)$$

R (also used as λ) is the finite rate of increase:

$R < 1$ declining N,

$R = 1$ unchanging N,

$R > 1$ increasing N.

$R = 1.2$ N increases by 20% every year.

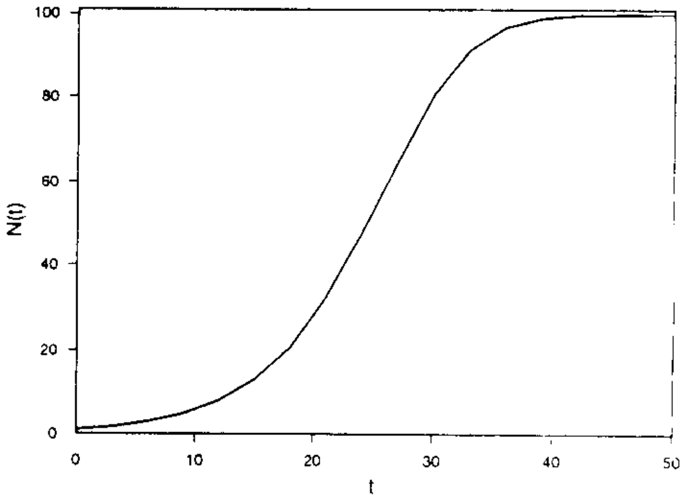
Density dependence at high densities

Growth rate declines at high population densities due to intra-specific competition, overcrowding, cannibalism, etc.

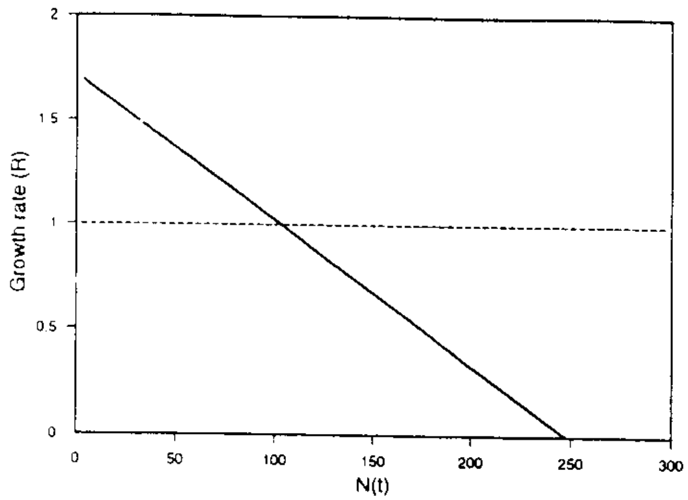
$$N(t+1) = f\,[\,N(t)\,]$$

$$N(t+1) = R\;N(t)$$

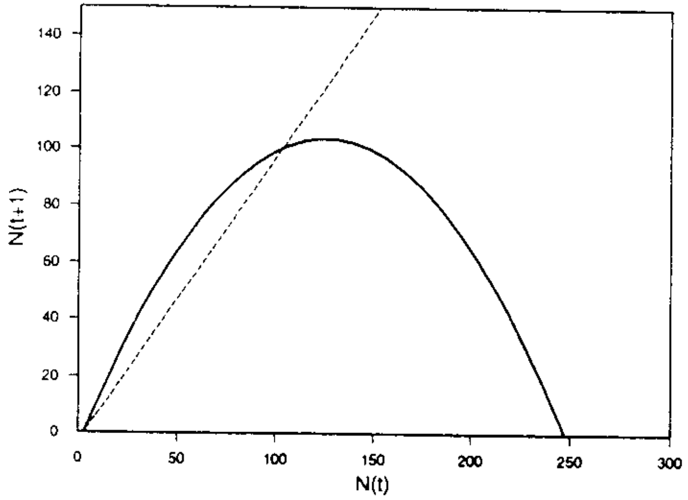
$$R = f\,[\,N(t)\,]$$



Population growth with density dependence



Density dependence of growth rate



Recruitment curve

Logistic function

Continuous time:

$$\frac{dN}{dt} = r \quad N$$

$$\frac{dN}{dt} = r \quad N \left(\frac{K-N}{K} \right)$$

Discrete time:

$$N(t+1) \quad = \quad f \; [\; N(t) \;]$$

$$N(t+1) \quad = \quad N(t) \left[1 \; + \; r \left(\frac{K-N(t)}{K} \right) \right]$$

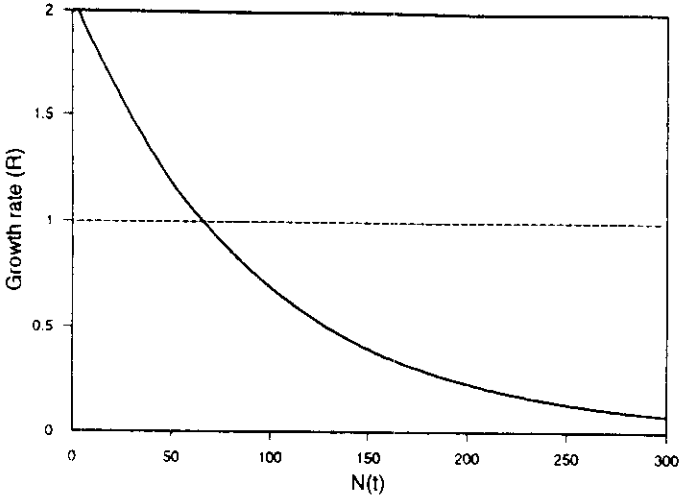
$$N(t+1) \quad = \quad N(t) \;\; e^{\left[\; r \left(\frac{K-N(t)}{K} \right) \right]}$$

Ricker equation:

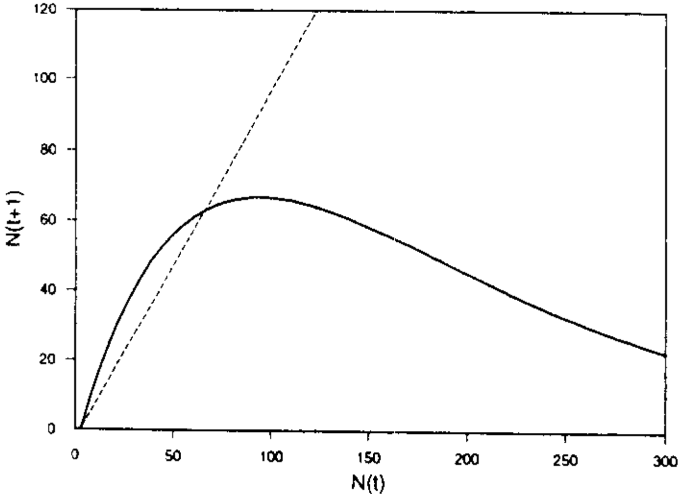
$$N(t+1) \quad = \quad N(t) \quad R \quad e^{-\beta \; N(t)}$$

$$R = e^{r}$$

$$\beta = \ln(R)/K$$



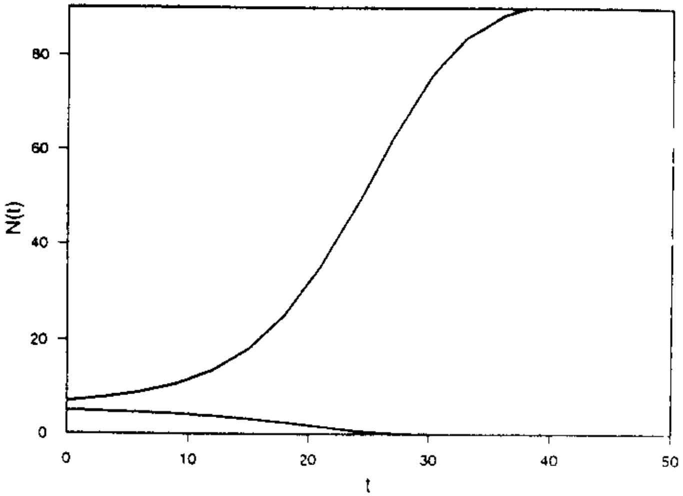
Density dependence of growth rate



Recruitment curve

Density dependence at low densities

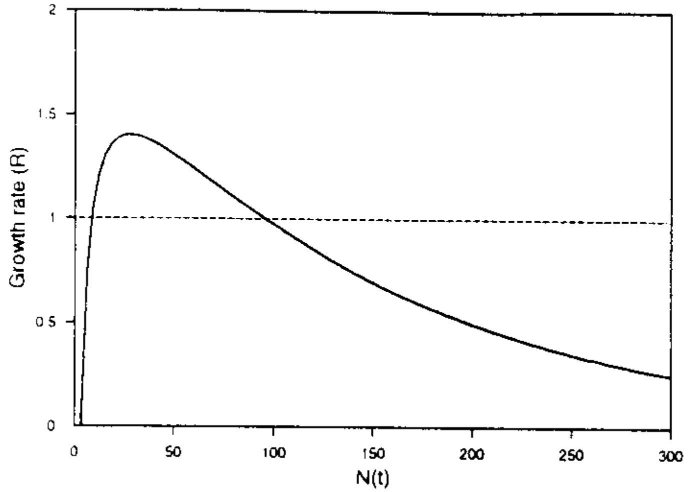
Alee effects: Growth rate declines at low population densities due to inbreeding depression, difficulty in finding mates, etc.



Population growth with Allee effects

$$N(t+1) \quad = \quad N(t)\ R\ \left(\frac{N(t)}{A+N(t)}\right)$$

$$N(t+1) \quad = \quad N(t)\ R\ e^{(-\beta\ N(t))}\left(\frac{N(t)}{A+N(t)}\right)$$



Density dependence of growth rate

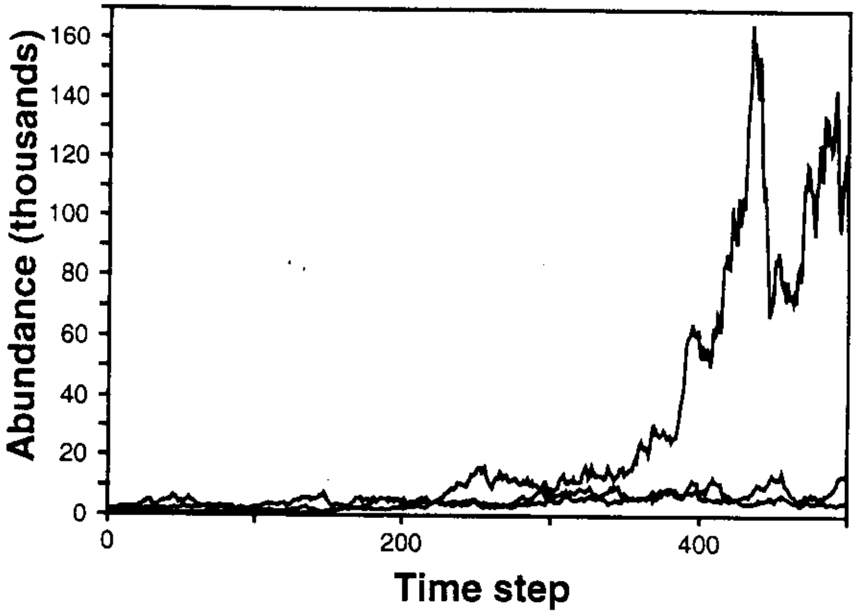
Environmental Stochasticity

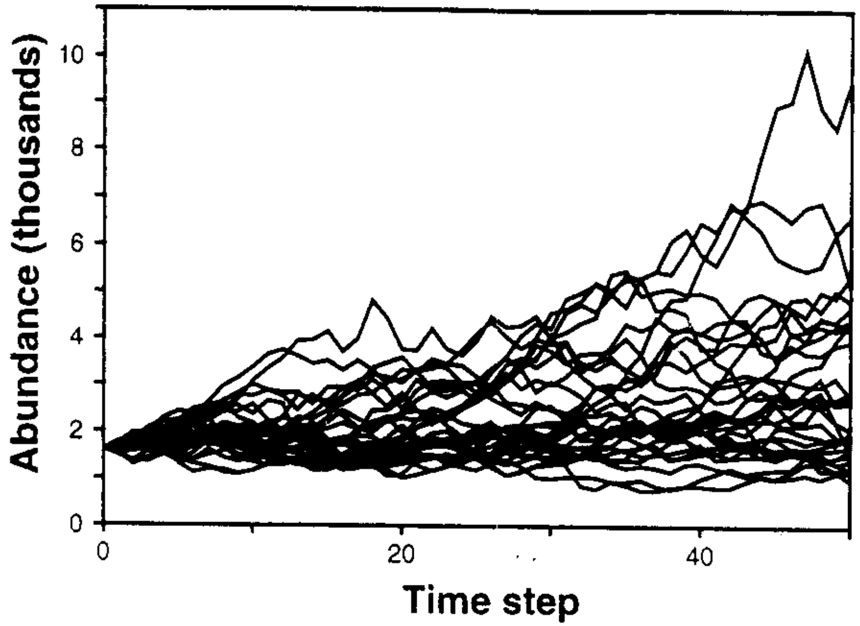
Temporal variation in parameters due to fluctuations in environmental variables

$$N(t+1) \quad = \quad R \quad N(t)$$

$$N(t+1) \quad = \quad R(t) \quad N(t)$$

$$R(t) \quad = \quad \text{random} \; (\; \overline{R} \; , \; \sigma \;)$$





Risk Analysis

Risk of extinction or decline

Chance of recovery

Time to extinction or decline

Time to recovery

Age structure

Demographic characteristics (survivorship, fecundity, dispersal) vary with age

$$\mathbf{N} = \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \end{bmatrix}.$$

Variables:

Survivorship from age x to age $x+1$: S_x

Fecundity of individuals at age x: F_x

Population growth:

$$N_1(t+1) = N_0(t) \;\; S_0$$

$$N_2(t+1) = N_1(t) \;\; S_1$$

$$N_3(t+1) = N_2(t) \;\; S_2$$

$$\ldots$$

$$N_0(t+1) = \sum_{x=1}^{\omega} F_x(t) \;\; N_x(t)$$

Leslie matrix:

$$\mathbf{L} = \begin{bmatrix} F_0 & F_1 & F_2 & F_3 \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & 0 \end{bmatrix}.$$

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \\ N_2(t+1) \\ N_3(t+1) \end{bmatrix} = \begin{bmatrix} F_0 & F_1 & F_2 & F_3 \\ S_0 & 0 & 0 & 0 \\ 0 & S_1 & 0 & 0 \\ 0 & 0 & S_2 & 0 \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \\ N_3(t) \end{bmatrix}$$

$$\mathbf{N}(t+1) = \mathbf{L}\,\mathbf{N}(t)$$

Environmental Stochasticity

Temporal variation in survivorships and fecundities due to fluctuations in environmental variables

$$\mathbf{L} = \begin{bmatrix} F_0(t) & F_1(t) & F_2(t) & F_3(t) \\ S_0(t) & 0 & 0 & 0 \\ 0 & S_1(t) & 0 & 0 \\ 0 & 0 & S_2(t) & 0 \end{bmatrix}.$$

$S_x(t)$ = random ($\overline{S}_x$, σ_S)

$F_x(t)$ = random ($\overline{F}_x$, σ_F)

Correlations among parameters:	Covar(S, F)
("good" and "bad" years)	Covar(S_1, S_2)

Alternative: matrix selection

select among limited number of observed matrices at random

Demographic Stochasticity

Assume:

(i) there is no environmental variation; vital rates (survivorships) remain constant

(ii) $S_2 = 0.4$

$$N_3(t+1) \; = \; N_2(t) \;\; S_2$$

$$N_2(t) = 100 \Rightarrow \;\; N_3(t+1) \; = \; 100 \cdot 0.4 \; \approx \; 40$$

$$N_2(t) = 3 \;\; \Rightarrow \;\; N_3(t+1) \; = \; 3 \cdot 0.4 \; \approx \; 1.2?$$

If each of the three individuals have 40% chance of surviving winter, and if their survival is independent, then

P (all surviving) = $0.4 \cdot 0.4 \cdot 0.4 = 0.4^3$

P (none surviving) = $(1-0.4) \cdot (1-0.4) \cdot (1-0.4) = (1-0.4)^3$

$$\Rightarrow \;\; N_3(t+1) \; = \; (0, 1, 2, 3)$$

$$N_3(t+1) \; = \; \text{binomial}(\; 3 \;,\; 0.4 \;)$$

$$N_x(t+1) \; = \; \text{binomial}(\; N_{x-1}(t) \;,\; S_{x-1} \;)$$

Number of young $=$ Poisson($N_x(t) \cdot F_x$)

Stage structure

eggs, larvae, pupae and adults

juvenile, non-breeding adult, breeding adult

seeds, seedlings, saplings, understory and canopy trees

$$\mathbf{N}(t+1) \; = \; \begin{bmatrix} p_{00} & p_{01} & p_{02} & \cdot & \cdot & \cdot & p_{0\omega} \\ p_{10} & p_{11} & p_{12} & \cdot & \cdot & \cdot & p_{1\omega} \\ p_{20} & p_{21} & p_{22} & \cdot & \cdot & \cdot & p_{2\omega} \\ \cdot & \cdot & \cdot & & & & \cdot \\ \cdot & \cdot & \cdot & & & & \cdot \\ \cdot & \cdot & \cdot & & & & \cdot \\ p_{\omega 0} & p_{\omega 1} & p_{\omega 2} & \cdot & \cdot & \cdot & p_{\omega\omega} \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \\ \\ \cdot \\ \cdot \\ N_\omega(t) \end{bmatrix}$$

Criteria:

demography depends on physiological stage, and development into these stages is not consistent in time among individuals,

demography depends on size or vigor and growth is plastic,

some individuals exhibit retarded or accelerated development or regression,

the ages of individuals cannot be determined, and

equal-width classes lead to computational inefficiency.

Example: loggerhead sea turtle

The loggerhead sea turtle *Caretta caretta*:

long-lived iteroparous marine turtle
a threatened species
difficult to age

Stage-structured model (Crouse *et al.* 1987):

(1) first-year individuals (eggs and hatchlings),
(2) small juveniles,
(3) large juveniles,
(4) subadults,
(5) novice breeders,
(6) first-year remigrants, and
(7) mature breeders.

The projection matrix:

	1	2	3	4	5	6	7
1	0	0	0	0	127	4	80
2	0.6747	0.7370	0	0	0	0	0
3	0	0.0486	0.6610	0	0	0	0
4	0	0	0.0147	0.6907	0	0	0
5	0	0	0	0.0518	0	0	0
6	0	0	0	0	0.8091	0	0
7	0	0	0	0	0	0.8091	0.8089

Asymptotic statistics

Limited importance in conservation biology, but still commonly discussed in the literature.

The dominant eigenvector λ of the transition matrix:

asymptotic finite growth rate of the population growing
assumes matrix is unchanging,
i.e., there is no density dependence, trends, or stochasticity

Stable age distribution:

the vector of relative abundances in each stage or age class
approached if projection matrix remains unchanged
right eigenvector of the matrix corresponding to the dominant eigenvalue

Reproductive value:

the vector giving reproductive output of an average individual in a given age/stage
left eigenvector of the matrix corresponding to the dominant eigenvalue

Sensitivity analyses

Sensitivities: How a population's asymptotic growth rate depends on the elements of the projection matrix (Caswell 1978)

Assuming the projection matrix is fixed over time:

partial derivative of the dominant eigenvalue λ with respect to the value of an element,

$$s_{xy} = \frac{\partial \lambda}{\partial p_{xy}} = \frac{v_x u_y}{\sum_z u_z v_z}$$

where p_{xy} is the element in the xth row and yth column of the matrix and v and u are the left and right eigenvectors of the matrix, respectively.

Elasticities: proportional sensitivities (Kroon *et al.* 1986)

Sensitivity can be very large even though the matrix element is 0

(babies making babies => very high birth rate)

sometimes irrelevant

$$e_{xy} = \frac{p_{xy}}{\lambda} s_{xy}.$$

Elasticities are measures of the contribution each transition coefficient makes to the dominant eigenvalue.

All the elasticities in a matrix sum to one

The column-sums (equal to the corresponding row-sums) measure the total contribution of the age class as a whole to the population growth rate, synthesizing its fecundity, survival and transition rates into a single scalar.

Disadvantages:

assume infinitesimal changes in the parameters

ignore interactions (assume that effect of changes in two parameters are additive)

rely on λ instead more relevant measures, such as extinction risk, time to extinction, or chance of recovery

Uses of sensitivity analyses

helps empiricists decide which vital rates to measure especially carefully

planning optimal conservation or management strategies

(is it better to reduce poaching of adults, or to modify habitat to enhance survival of juveniles?)

designing nature reserves

SLOSS

nearby or far away

Density dependence

Change in vital rates as a function of population density

Decisions:

- vital rate(s) that depend on density
- form of the function
- arguments of the function
- parameters of the function

e.g., Survivorship S_x,

Fecundity F_x, or

Total fecundity $\sum_{x=1}^{\omega} F_x N_x$

may change as N changes.

function may have a logistic form, include Allee effects, etc.

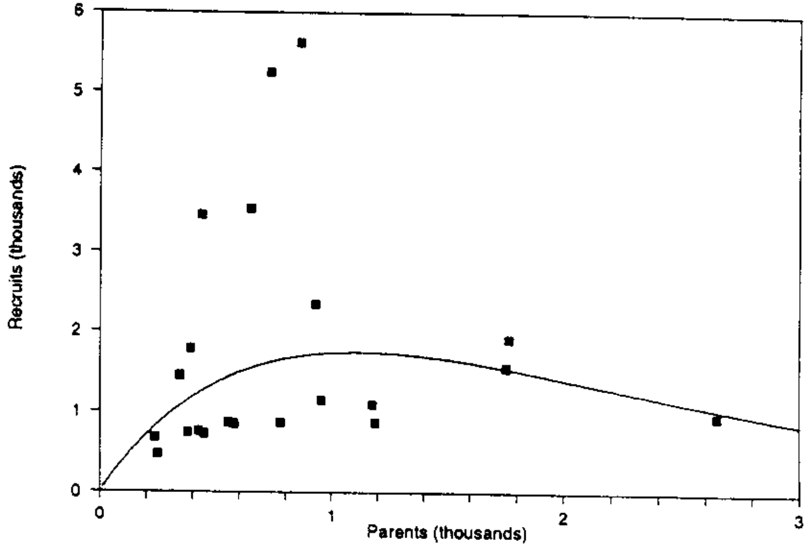
arguments may be total population size, or abundance in an age/stage class

simpler functions are easier to parameterize

Dealing with lack of data

Density independence is conservative (Ginzburg et al. 1990)

Observed relationships can be used



Scatter of data used as evidence for density dependence. Despite considerable fluctuation in the data points, very delicate curves are traditionally used to represent density dependence. (Redrawn from Ricker, 1975).

Importance of metapopulation dynamics in conservation biology

- Protection of species, not just single populations
- Sensitivity of extinction risk to spatial factors
- Fragmentation as a result of habitat loss
- Need to evaluate different types of impact
- Translocations and reintroductions
- Reserve design: Single large *vs.* several small populations (SLOSS)

Spatial heterogeneity and multiple populations

Heterogeneity of natural environments

Habitat fragmentation:
- Decrease in total area
- Increased isolation
- Smaller populations
- Increased edge effects

Factors affecting population extinction risk

Demography: Survivorship, fecundity, population growth rate

Age or stage structure

Density dependence

Environmental fluctuations

Demographic stochasticity

Additional factors affecting extinction risk in metapopulations

Number of populations

Geographic configuration

Spatial correlation

Migration patterns

Correlation of environmental variation

Correlated *vs.* independent extinctions

Geographically close populations (compared to distant populations):

- Correlated environments (increased extinction risk)
- Higher migration (decreased extinction risk)

Migration patterns

Biology of the species (e.g. dispersal ability)

Characteristics of the landscape (habitat corridors)

Distance-dependent migration

Directional migration

Density-dependent migration

Age, sex and genetic structure of the populations

Distance-dependent migration

Migration rate as negative exponential function of distance:

$$m_{ij} = e^{-d_{ij}/c}$$

m_{ij} = rate of migration (proportion of population *j* migrating per unit time to population *i*)

d_{ij} = distance between populations *i* and *j*

c = average distance a migrant travels

Density-dependent migration

- Higher tendency to emigrate under crowding
- Higher tendency to emigrate from small populations: stepping stone
- Dependence on density of target patch: Conspecific attraction

---

Interaction between factors

Combined effects of migration and correlation

Implications for SLOSS:

Geographically close populations (compared to distant populations):

- Correlated environments (increased extinction risk)
- Higher migration (decreased extinction risk)

Several small populations (compared to a single large populations):

- Higher demographic stochasticity (increased extinction risk)
- Amplified edge effects (increased extinction risk)
- Independent environments (decreased extinction risk)
- Recolonization possibility (decreased extinction risk)

METAPOPULATION MODELS

Island biogeography

Variable: Number of species

Parameters: Immigration and extinction rates

Occupancy models

Variable: Occupancy of patches by a species

Parameters: Migration and extinction probabilities

Population dynamic models

Variable: Number of individuals of a species in each patch

Parameters: Demographic variables, migration rates, spatial correlation

Levins' model

$$\mathrm{d}p/\mathrm{d}t = mp(1-p) - ep$$

$\mathrm{d}p/\mathrm{d}t$ = rate of change in the proportion of occupied patches

m = colonization probability from a patch to any other

e = extinction probability of a single patch

Colonization proportional to the product of occupied patches p and unoccupied patches $1-p$

Extinction proportional to the proportion of occupied patches.

The model has a positive equilibrium p^* if $m > e$:

$$p^* = 1 - e/m$$

Assumptions of the model

No local population dynamics

Infinite number of equal patches

Independent extinctions

Equal probability of migration

Generalizations of Levins' model

Effect of population size (Hanski 1983)

$$dp/dt = mp(1-p) - e(1-wp)p \qquad (5.3)$$

where w is a parameter describing the negative correlation between p and e.

Introducing correlated extinctions (Harrison & Quinn 1989):

1. There are two distinct extinction probabilities, corresponding to "good" and "bad" time steps. In a good year, extinction probability is $e = \mu - \delta$, in a bad year it is $e = \mu + \delta$ ...
2. The two types of time steps, good and bad, are equally probable.
3. The random component δ further divided into two components:

   $c\delta$ experienced by local populations in all patches,

   $(1-c)\delta$ varies independently among local populations.

Limitations of occupancy models

Unrealistic assumptions

Parameter estimation

A population dynamic model: RAMAS/space

Variables and parameters of the model

Variable: Number of individuals of a species in each patch

Parameters for single population dynamics: stochasticity, density dependence

Parameters for spatial structure: Migrations and correlated growth rates

Migrations

Migration-distance function

Directional migration

Correlations

Correlation-distance function

Assumptions and limitations

No age- or stage-structure

Genetics incorporated indirectly (e.g. through Allee effects)

Discrete time

Single species (interspecific interactions incorporated indirectly)

Extrinsic factors (social, economic) ignored