Dynamics of age-structured populations

Simon Levin

Princeton

SFI 2018

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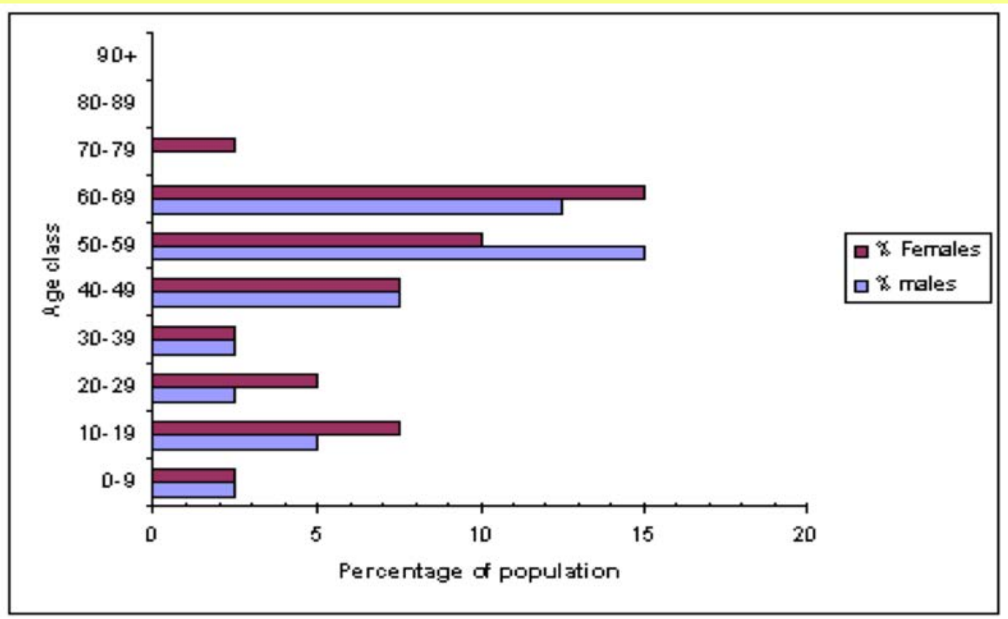
The formal roots of demography trace at least to John Graunt, 17th Century



www.sbs.utexas.edu/jcabbott

John Graunt

The Di[illegible] and Casualties this Week.

Abortive	4	Lethargy	1
Aged	39	Overlaid	1
Ague	3	Plurisie	2
Brused	1	Quinsie	3
Burnt (an Infant) by accident at St. Alhallowes Great	1	Rickets	7
Cancer	1	Rising of the Lights	4
Childbed	4	Rupture	1
Chrisomes	15	Scowring	2
Consumption	78	Scurvy	2
Convulsion	25	Spleen	1
Distracted	1	Spotted feaver	2
Dropsie	23	Stilborn	10
Feaver	37	Stopping of the Stomach	6
Flox and Small-pox	21	Suddenly	2
Flux	1	Surfet	4
French-pox	1	Teeth	29
Gowt	2	Threw himself out of a window (being Distracted) at St. Clement Eastcheap	1
Griping in the guts	20	Thrush	1
Jaundies	4	Tissick	2
Impostum	2	Ulcer	1
Infants	14	Winde	2
Kingsevill	2		

Born and Christned { Males 109, Females 102, In all 211 } Buried { Males 194, Females 189, In all 383 } Plague 0

Increased in the Burials this week — 34

Parishes Clear of the Plague — 130 Parishes Infected — 0

The Assise of Bread set forth by Order of the Lord Maior and Court of Aldermen, A Penny Wheaten loaf [illegible] contain 5 Ounces and three half penny White loaves the like weight.

Guildhall Museum Library, London

Rising of the lights

A New Booke of Mistakes (1637), Robert Chamberlain wrote an epitaph

- Of one Parkins a boone Companion in Essex who dyed of the rising of the Lights.
  - Poore Parkins, now percust here lies,
    Light hearted, till his Lights did rise.
    Lights of the Body, are the Bellowes,
    And hee, one of the best good fellowes
    That Essex yeelded, (all we do know)
    And breath'd, till they did cease to blow.

Wikipedia

John Graunt (1620-1674)

Population of London should double every 56-64 years.

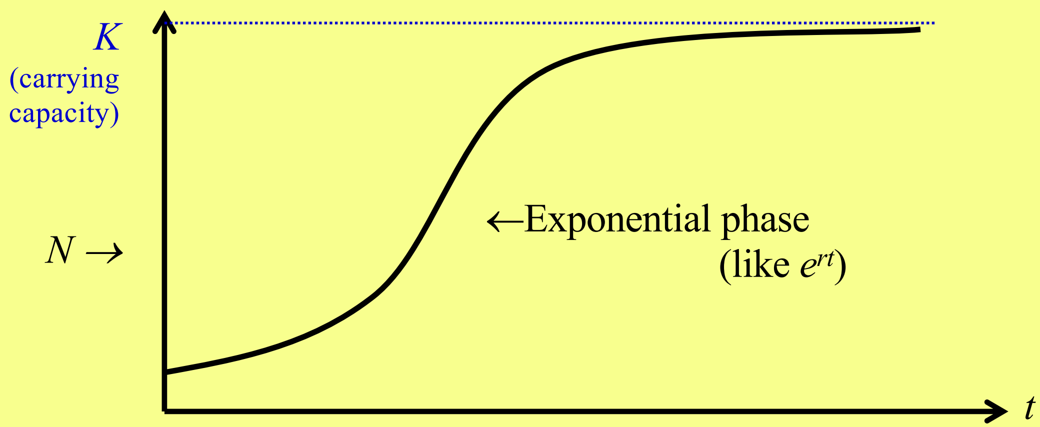
If this had been going on since Adam and Eve, population size would be~10^{26}

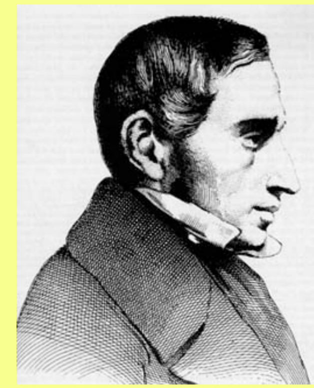
$\longrightarrow$ 100 million people /sq. cm.

Populations cannot grow without bound

Thomas Malthus (1766-1834)

Population growth, resources limited





Verhulst

r describes growth at low densities

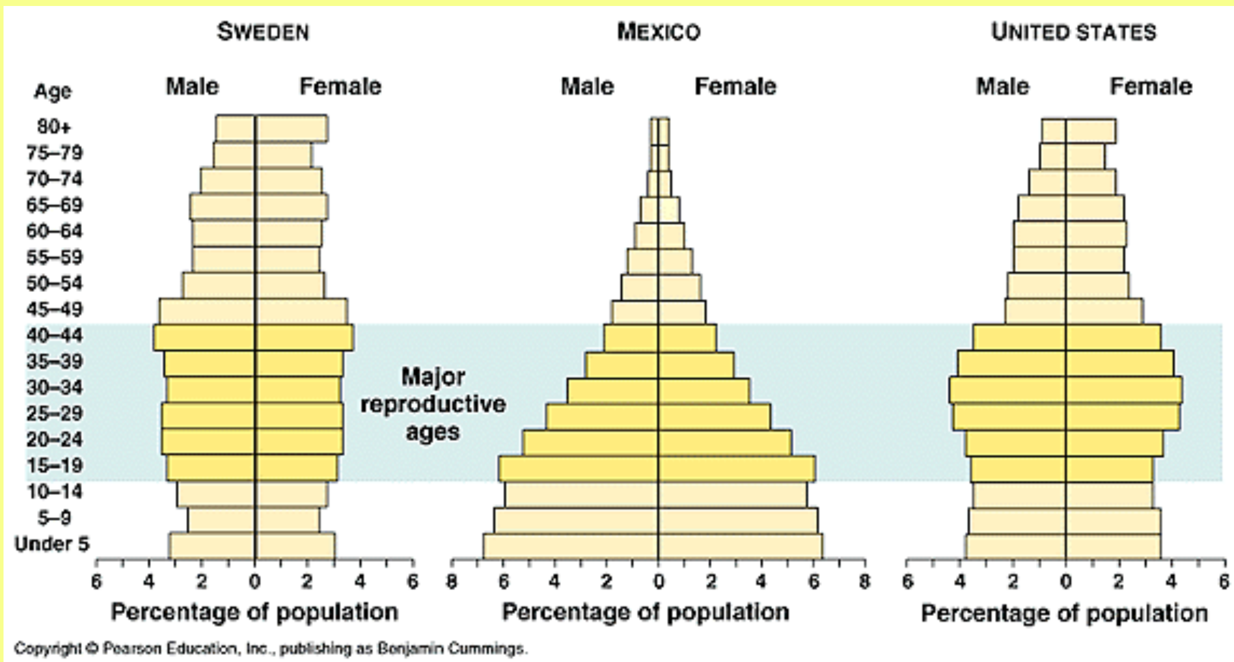
K determines growth at high densities

r : colonist : high growth rate, low competitive ability, small body size, high dispersal

K : competitive dominants: low growth rate, high competitive ability, large body size, low dispersal

Discrete time: overshoot possible, potential for chaos

Age structure is fundamental, ecologically and evolutionarily



Fibonacci

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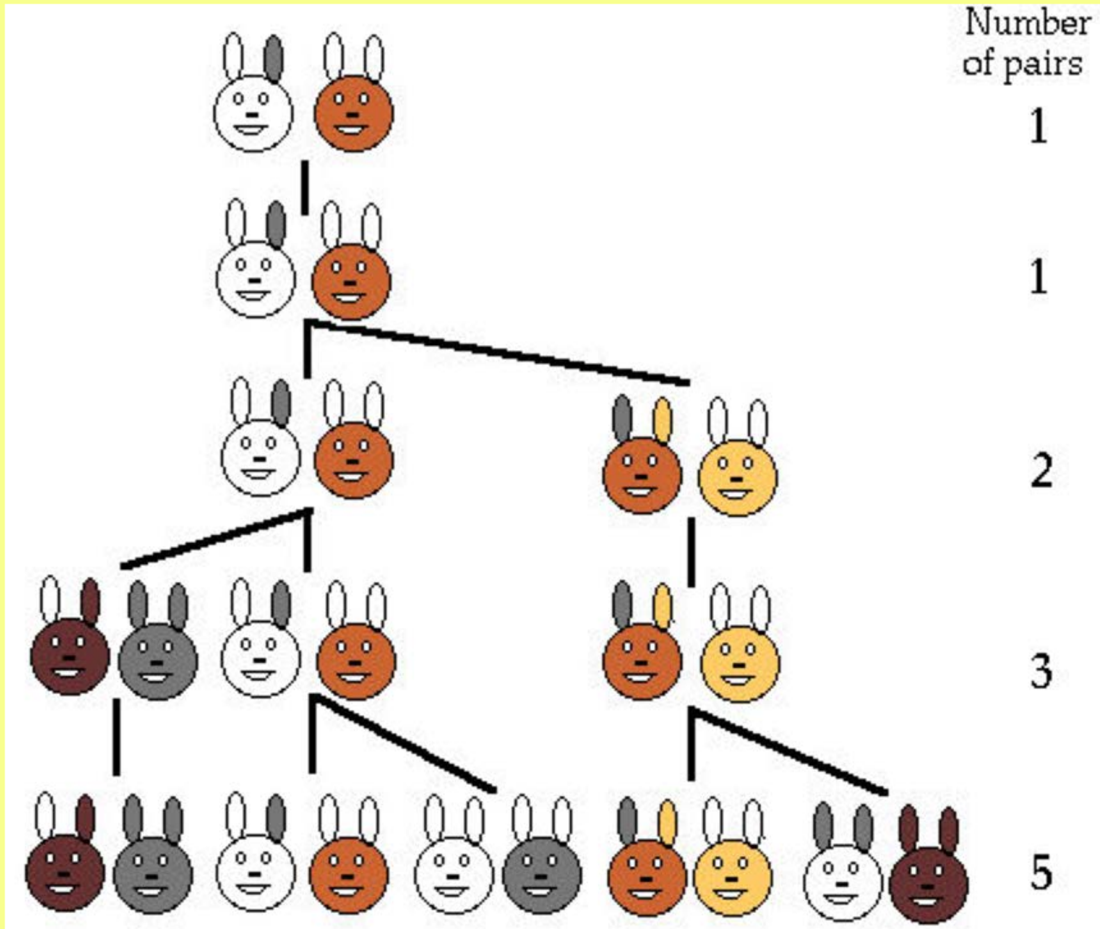


Population sizes form Fibonacci sequence
1, 1, 2, 3, 5, 8, 13, 21, 34, 55, …

Year	Young	Old	Y/(Y+O
0	1	0	1.00
1	1	1	0.50
2	2	1	0.67
3	3	2	0.60
4	5	3	0.63
5	8	5	0.62
6	13	8	0.62
7	21	13	0.62
8	34	21	0.62
9	55	34	0.62

Population assumes "stable age distribution," and each age class grows asymptiotically at the same rate $(1+\sqrt{5})/2$

This is a trivial application of deep methodology: L is the Leslie matrix

age-specific fecundities..assume no periodic fecundity

$$\mathbf{L} = \begin{bmatrix} f_0 & f_1 & \cdots & f_{A-1} & f_A \\ p_0 & 0 & \cdots & 0 & 0 \\ 0 & p_1 & \cdots & 0 & 0 \\ \cdot & \cdot & \cdots & \cdot & \cdot \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & p_{A-1} & 0 \end{bmatrix}$$

Note: $p_A = 0$, by definition

Between-age survivorship probabilities

Simplifying the notation, we can refer to these populations in vector format

$$\vec{n}_{t+1} = \begin{bmatrix} n_{0,\, t+1} \\ n_{1,\, t+1} \\ \vdots \\ n_{A-1,t+1} \\ n_{A,\, t+1} \end{bmatrix}$$

Projection

$$\vec{n}_{t+1} = L\vec{n}_t$$

And under conditions of constant life history parameters, we know that the population reaches a *stable age distribution* fitting...

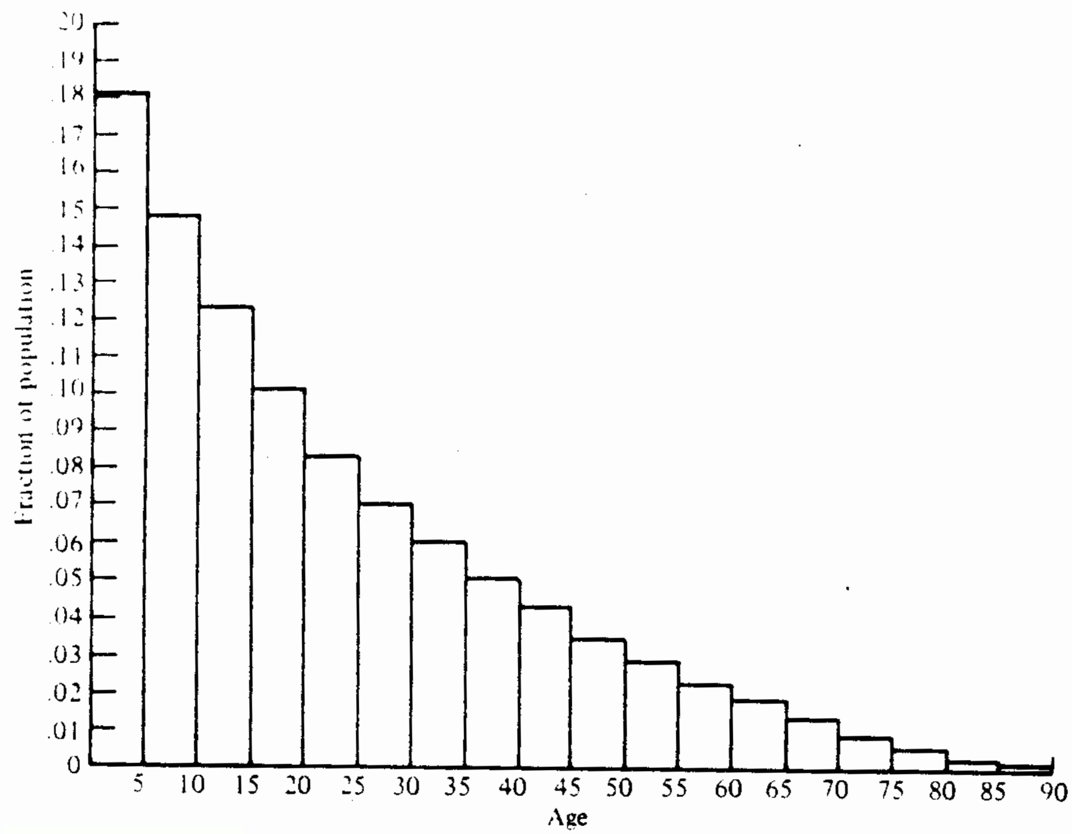
$$\vec{n}_{t+1} = \lambda \vec{n}_t = \begin{bmatrix} \lambda n_{0,t} \\ \lambda n_{1,t} \\ \vdots \\ \lambda n_{A-1,t} \\ \lambda n_{A,t} \end{bmatrix}$$

where every age class has the identical growth rate, λ.

A **stable age distribution** means that the relative proportions of all age classes stay the same

and also that every age class grows by a factor λ each year.

In general, for constant life table, population will settle into a stable age distribution.



. *Age distribution for females in Mexico in* 1966. *Note the comparatively higher proportion of young people in Mexico as compared with Spain.* [Data from N. Keyfitz, and W. Flieger (1971), *Population, Facts and Methods of Demography*, W. H. Freeman and Company, Publishers, San Francisco.]

From Leslie matrix, can find

- λ ("dominant eigenvalue" of L)
- Stable age distribution ("dominant eigenvector")
- λ is the root of the matrix's "characteristic equation"

$$\mathbf{1 = \Sigma}\, \boldsymbol{l_x f_x \lambda^{-x-1}}$$

- $\boldsymbol{f_x = p_x m_{x+1}}$

$$\mathbf{1 = \Sigma}\, \boldsymbol{l_x\ m_x\ \lambda^{-x}}$$

Later theory extended these considerations to continuous age/time

- Renewal theory

$$n(t) = \int_0^t n(t-u)l(u)m(u)du$$

- McKendrick-vonFoerster

$$\partial n(a,t)/\partial t = -\partial n(a,t)/\partial a - \mu(a,t)n(a,t)$$

How do we find stable age distribution?

In a stable age distribution, if
there are B births this year,
there were B/λ last year
B/λ^2 two years ago
B/λ^3 three years ago
etc.

Stable age structure

Age	Number of cohort	Number alive today
0	B	Bl_0
1	B/λ	Bl_1/λ
2	B/λ^2	Bl_2/λ^2
3	B/λ^3	Bl_3/λ^3
4	B/λ^4	Bl_4/λ^4
5	B/λ^5	Bl_5/λ^5

Births this year …

to individuals of age	Number of births
0	Bl_0m_0
1	Bl_1m_1/λ
2	Bl_2m_2/λ^2
3	Bl_3m_3/λ^3
4	Bl_4m_4/λ^4
5	Bl_5m_5/λ^5
Total	B

So $$B = B\sum l_x m_x \lambda^{-x}$$ Euler's equation $$1 = \sum l_x m_x \lambda^{-x}$$

Summary: Euler's Equation

Given l_x, m_x, λ is the root of

$$1 = \sum l_x m_x \lambda^{-x}$$

Since $\lambda = e^r$

$$1 = \sum l_x m_x e^{-rx}$$

Analytically, these may be in most cases impossible to solve. However, on a computer, it is easy to find λ or r.

Review:

A population with a fixed l_x, m_x schedule has a fixed
Leslie matrix.

Hence, it (in general) tends to a stable age distribution, in which every age class grows by the same factor λ ($r = ln\ \lambda$). *There are a few minor exceptions_

λ can be found by simulation, or by solving Euler's equation

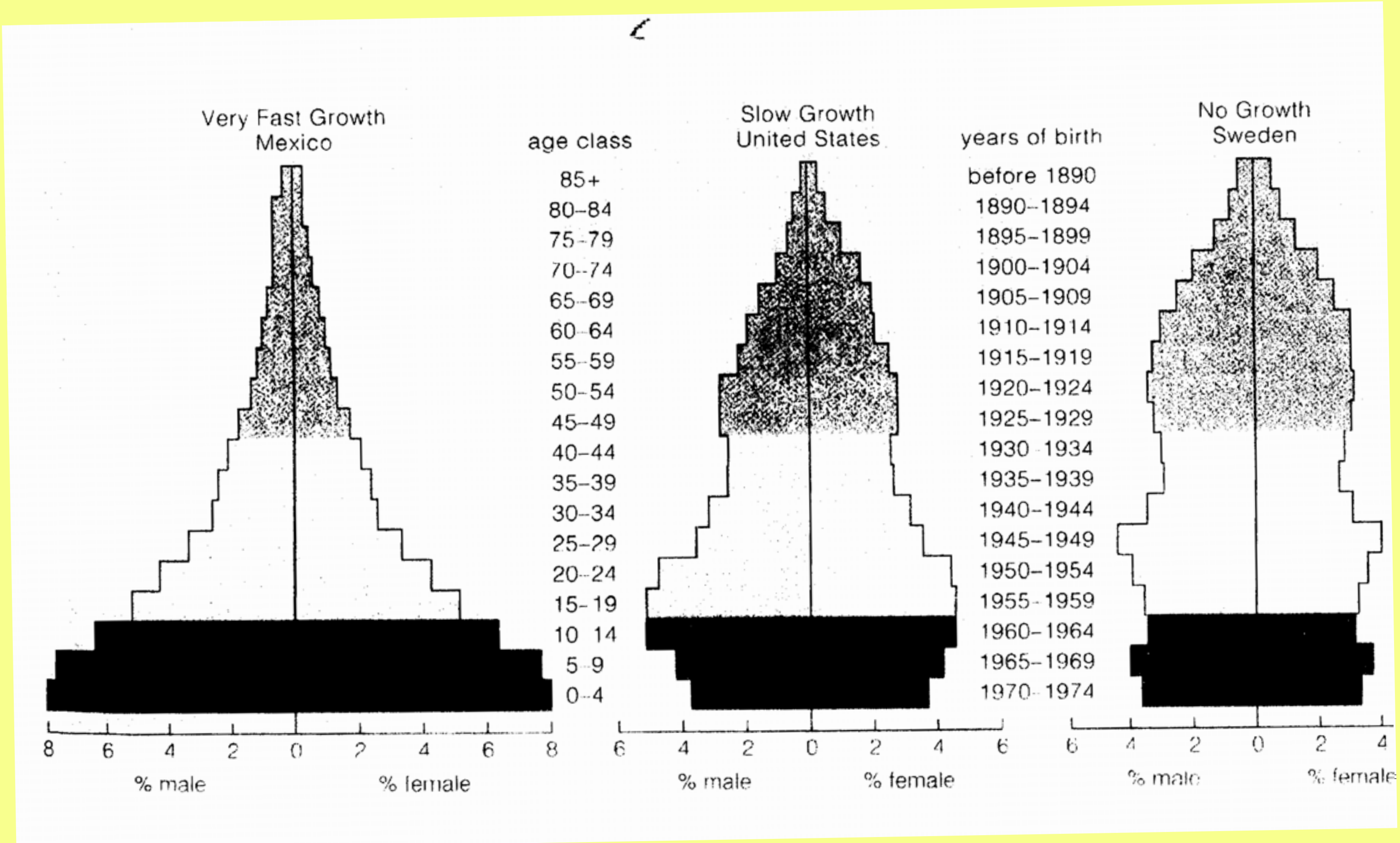
$$1 = \sum l_x m_x \lambda^{-x}$$

But there may be long transients before stable age distribution is reached.

And in a fluctuating environment, it may never be even approximately achieved.

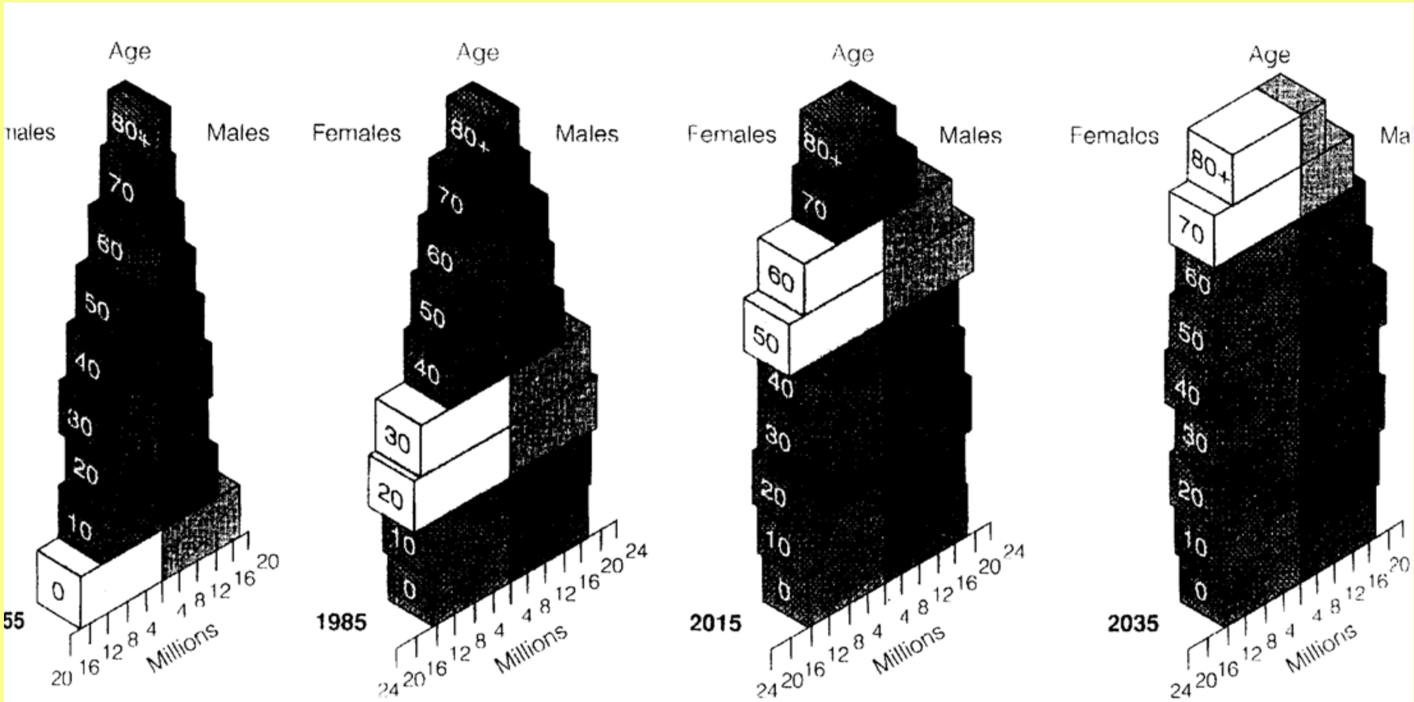
Euler-Lotka, continuous time
Implicit definition of r

$$1 = \int_0^\infty e^{-ra} l(a) b(a) da$$



Very Fast Growth
Mexico
age class
Slow Growth
United States
years of birth
No Growth
Sweden
85+
80–84
75–79
70–74
65–69
60–64
55–59
50–54
45–49
40–44
35–39
30–34
25–29
20–24
15–19
10–14
5–9
0–4
before 1890
1890–1894
1895–1899
1900–1904
1905–1909
1910–1914
1915–1919
1920–1924
1925–1929
1930–1934
1935–1939
1940–1944
1945–1949
1950–1954
1955–1959
1960–1964
1965–1969
1970–1974
8 6 4 2 0 2 4 6 8
6 4 2 0 2 4 6
6 4 2 0 2 4
% male
% female

Away from stable age distribution



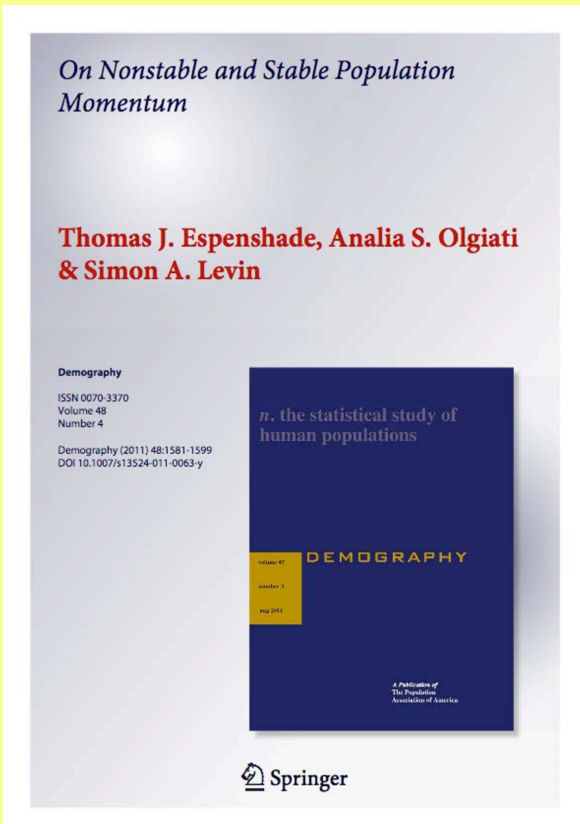
Tracking the baby-boom generation. Age structure of the U.S. population in 1955, 1985, 2015, and 2035 (data from the Population Reference Bureau and U.S. Census Bureau).

Population momentum is encapsulated either in

- How far the age structure is from stable age distribution

- How far the average relative reproductive value is from what it would be in stable age distribution

Population momentum



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Population Momentum Across the Demographic Transition

Laura Blue and **Thomas J. Espenshade**

A typical consequence of the demographic transition—a population's shift from high mortality and high fertility to low mortality and low fertility—is a period of robust population growth. This growth occurs once survival has improved but before fertility has fallen to or below replacement level, so that the birth rate substantially exceeds the death rate. During the second half of the twentieth century, the world experienced unprecedented population growth as developing countries underwent a demographic transition. It was during this period that Nathan Keyfitz demonstrated how an immediate drop to replacement fertility in high-fertility populations could still result in decades of population growth. Building on work by Paul Vincent (1945), he called this outcome "population momentum." Keyfitz wrote, "The phenomenon occurs because a history of high fertility has resulted in a high proportion of women in the reproductive ages, and these ensure high crude birth rates long after the age-specific rates have dropped" (Keyfitz 1971: 71).

For societies today that have not yet completed their demographic transitions, population momentum is still expected to contribute significantly to future growth, as relatively large cohorts of children enter their reproductive years and bear children. John Bongaarts (1994 1999) calculated that population momentum will account for about half of the developing world's projected twenty-first-century population growth. However, even though momentum is a useful concept precisely because of the non-stationary age structures that exist in populations in the midst of demographic transition, no research has examined trends in momentum or documented the highly regular pattern of population momentum across the demographic transition. This article sets out to do so.

We describe the arc of population momentum over time in 16 populations: five in the now-developed world and 11 in the developing world. Because population momentum identifies the cumulative future contribution of today's age distribution to a population's growth and size, adding momentum to our understanding of demographic transition means that we do not treat changes in age distribution merely as a consequence of demographic transition, as is usually the case (Lee 2003). Instead, we also illustrate the impact that these age-distribution changes have themselves had in producing key features of the demographic transition. Age composition exerts an independent influence on crude birth and crude death rates so that for given vital rate schedules, population growth rates are typically highest in those populations with a "middle-heavy" age distribution. During demographic transition (or even during a demographic crisis), any change in a population's age distribution will have repercussions for future population growth potential and future population size.

We also trace the course of two recently defined measures of population momentum. Espenshade, Olgiati, and Levin (2011) decompose total momentum into two constituent and multiplicative parts: "stable" momentum measures deviations between the stable age distribution implied by the population's mortality and fertility and the stationary age distribution implied by the population's death rates; and "nonstable" momentum measures

Figures in this article are available in color in the electronic edition of the journal.

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Life tables and population growth

- A survivorship curve summarizes the pattern of survival in a population
- A maternity (fecundity) schedule summarizes reproductive patterns
- The age distribution of a population reflects its history of survival, reproduction and potential for future growth

Relative reproductive value

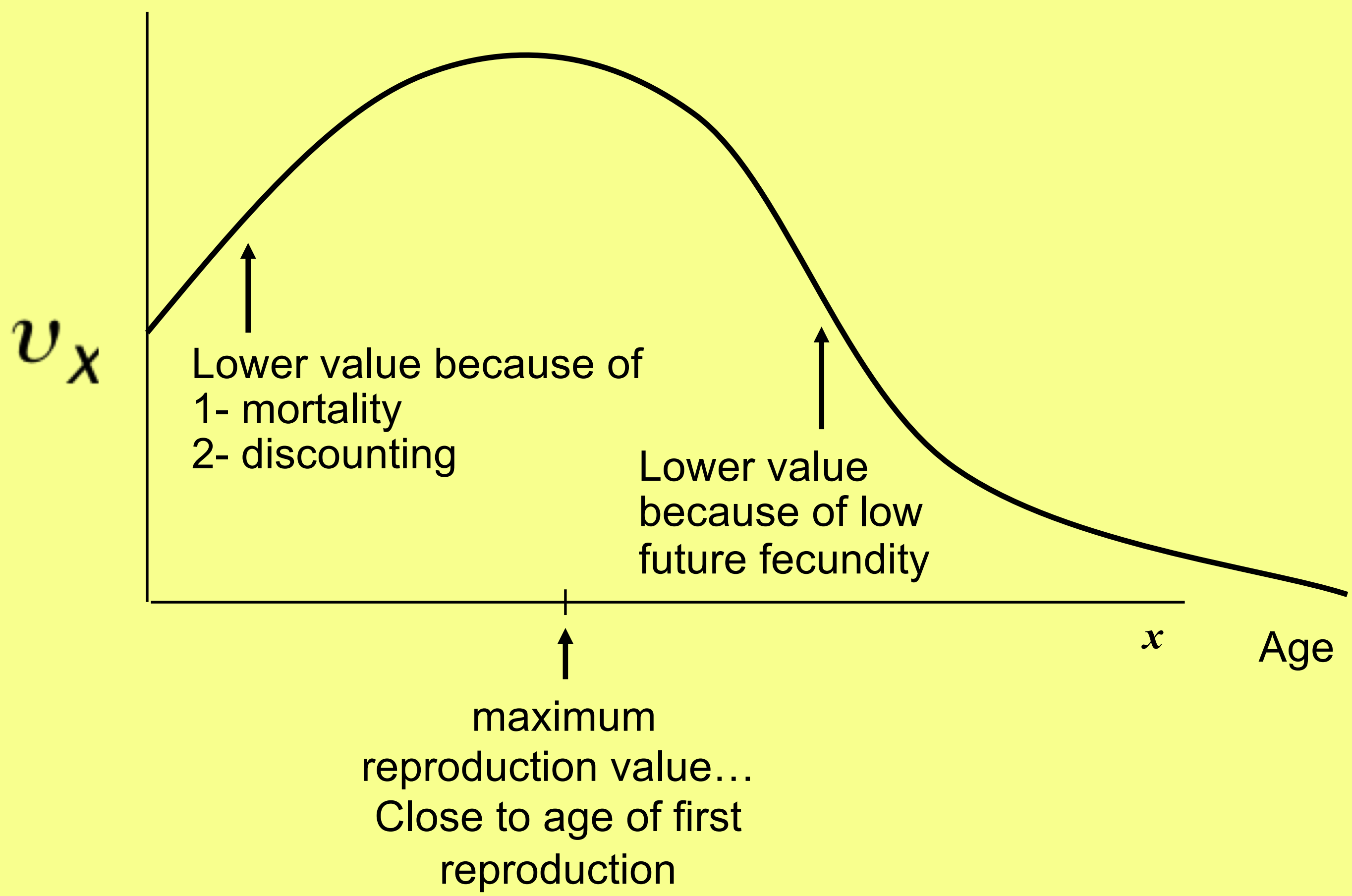
Maternity
at *y*

$$v_x = \sum_{y=x}^{\infty} \left(\frac{l_y}{l_x} \right) m_y \lambda^{x-y}$$

Discounting
for future

Probability of
surviving from
x to *y*

Typical pattern for reproductive value



Consequences

- The force of evolution is strongest where the relative reproductive value is greatest
- Hence post-reproductive mortality may be high
- Infant mortality may be high

How has evolution shaped

- Our personal and societal discount rates?
- Our concern for others (prosociality)?
- Collective behavior and decision-making?
- Multicellularity and the emergence of societies?

- What are the consequences of this evolution?

Discounting and prosociality affect individual allocation strategies

Intergenerational resource transfers with random offspring numbers

Kenneth J. Arrow[a] **and Simon A. Levin**[b,1]

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Contributed by Kenneth J. Arrow, May 26, 2009 (sent for review March 29, 2009)

A problem common to biology and economics is the transfer of resources from parents to children. We consider the issue under the assumption that the number of offspring is unknown and can be represented as a random variable. There are 3 basic assumptions. The first assumption is that a given body of resources can be divided into consumption (yielding satisfaction) and transfer to children. The second assumption is that the parents' welfare includes a concern for the welfare of their children; this is recursive in the sense that the children's welfares include concern for their children and so forth. However, the welfare of a child from a given consumption is counted somewhat differently (generally less) than that of the parent (the welfare of a child is "discounted"). The third assumption is that resources transferred may grow (or decline). In economic language, investment, including that in education or nutrition, is productive. Under suitable restrictions, precise formulas for the resulting allocation of resources are found, demonstrating that, depending on the shape of the utility curve, uncertainty regarding the number of offspring may or may not favor increased consumption. The results imply that wealth (stock of resources)

ping generations, offspring produced early in life are more valuable than those produced later because those offspring can also begin reproduction earlier. This is analogous to the classic investment problem in economics, in that population growth imposes a discount rate that affects when one should have offspring. The flip side is that early reproduction compromises the parent's ability to care for its children, and that increased number of offspring reduces the investment that can be made in each. Again, the best solution generally involves compromise and an intermediate optimum.

A particularly clear manifestation of this tradeoff involves the problem of clutch or litter size—how many offspring should an organism, say a bird, have in a particular litter? (11) Large litters mandate decreased investment in individuals, among other costs, but increase the number of lottery tickets in the evolutionary sweepstakes. This problem has relevance across the taxonomic spectrum, and especially from the production of seed by plants to the litter sizes of elephants and humans. Even for vertebrates, the evolutionary resolution shows great variation: The typical

ECONOMIC SCIENCES

Evolutionary theory also has a rich mathematical history

$$\Delta p = \left(\frac{pq}{2\bar{w}}\right)\left(\frac{d\bar{w}}{dp}\right)$$

Sewall Wright

R.A.Fisher

J.B.S.Haldane

The challenge remains to meld these two scales

Place ecological interactions within an evolutionary framework

Fast scale: $$dx/dt = f(x;\alpha,E)$$ Ecological

Slow scale: $$d\alpha/dt = \varepsilon g(x;\alpha,E)$$ Evolutionary

Approaches to marrying ecology and evolution

- Optimization
- Game Theory
- Coevolution
  - Tight
  - Diffuse

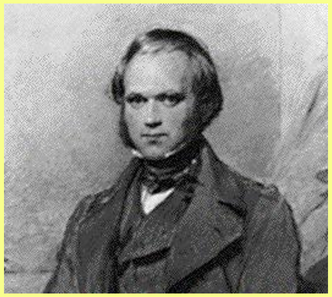
www.dkimages.com

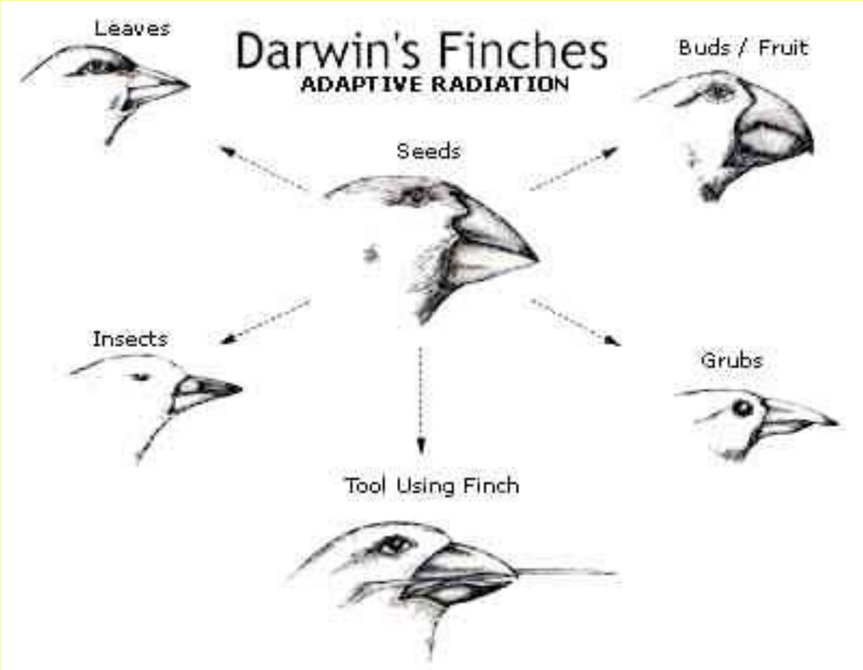
Evolution and the Theory of Games

"Evolution is an existentialist game"

LBSlobodkin

Darwin saw natural selection as a process of *gradual* adaptation in a changing environment





www.biology-online.org

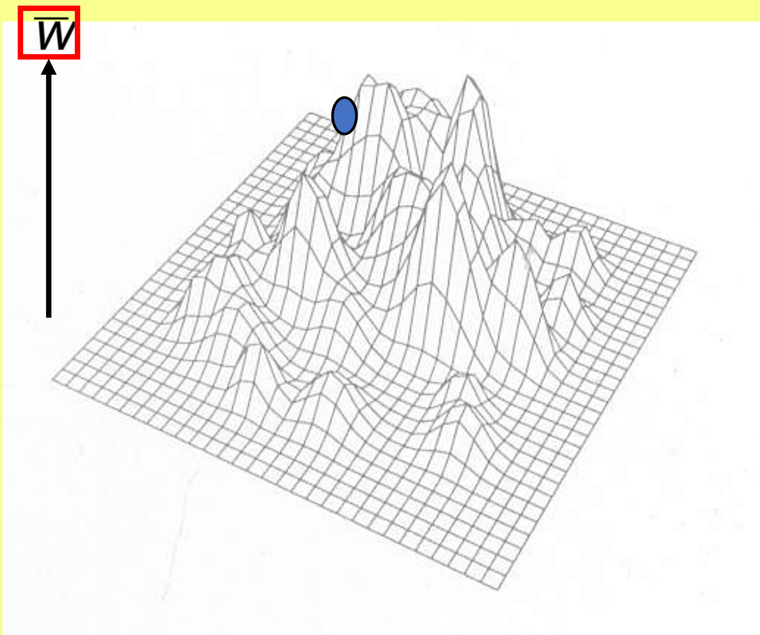
Too easily, however, this transmogrified into *Evolution as optimization*

www.thehitsdoctor.com

Why Optimization?

Selection as hill-climbing finds maxima

$$\boxed{d\overline{w}/dt = s(pq/\overline{w})(d\overline{w}/dp)^2}$$



Hence, an optimization principle emerges

But there are problems with this seductive picture

- Genetic constraints (epistasis, linkage)
- Temporal change in the landscape
- Frequency dependence
- Coevolution

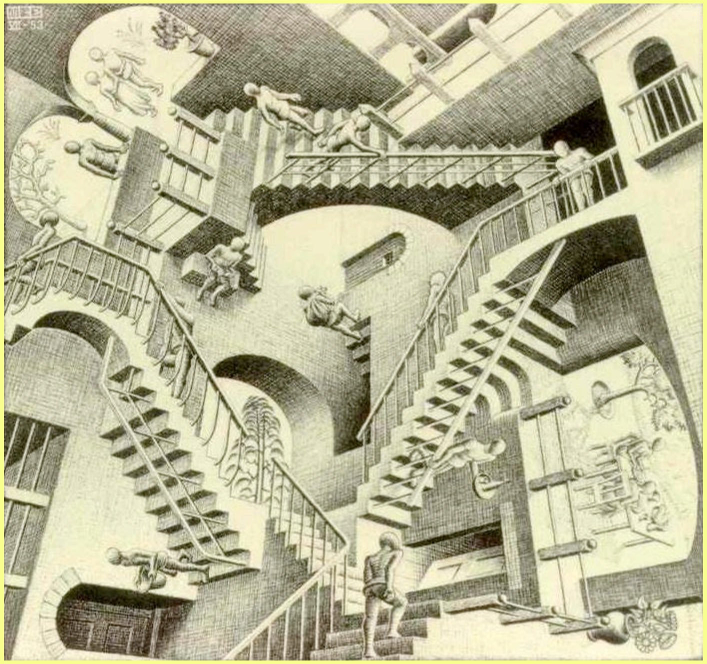
Indeed,

The deepest problems involve *frequency-dependence* and *coevolution*

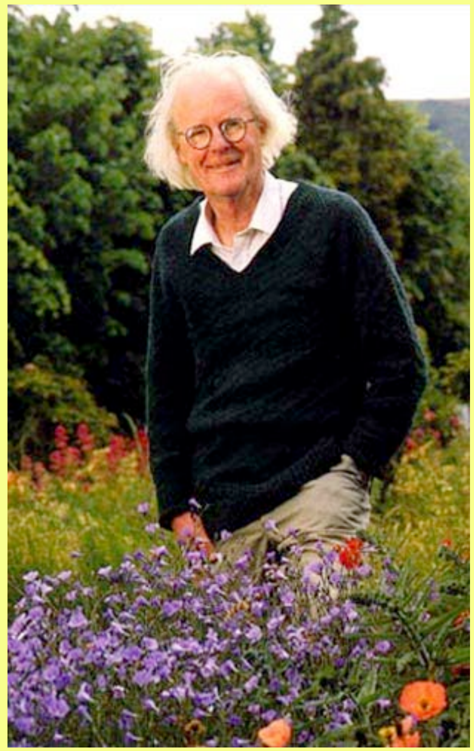
encyclopedia.laborlawtalk.com

Because of coevolution and frequency-dependence

- Optimization must give way to game theory



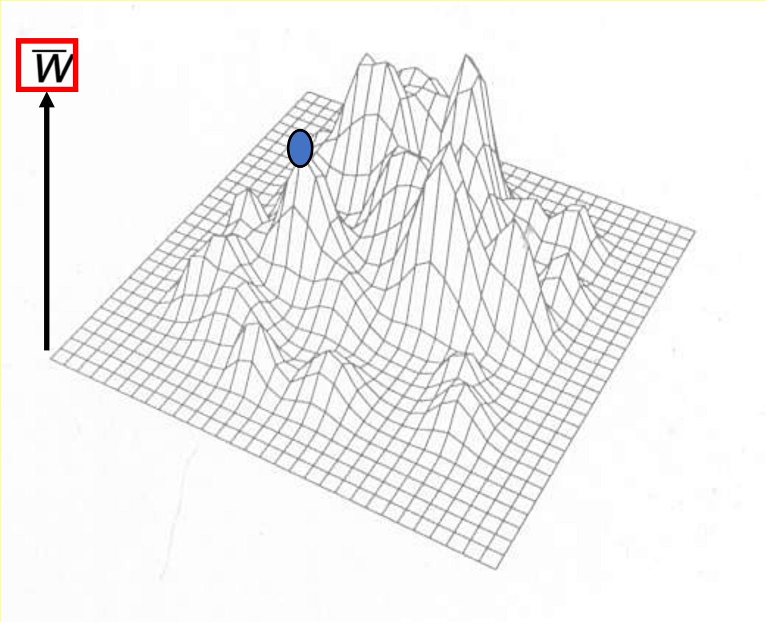
To deal with this,
Maynard Smith introduced the game-theoretic notion of the evolutionarily stable strategy (ESS):



www.pbs.org

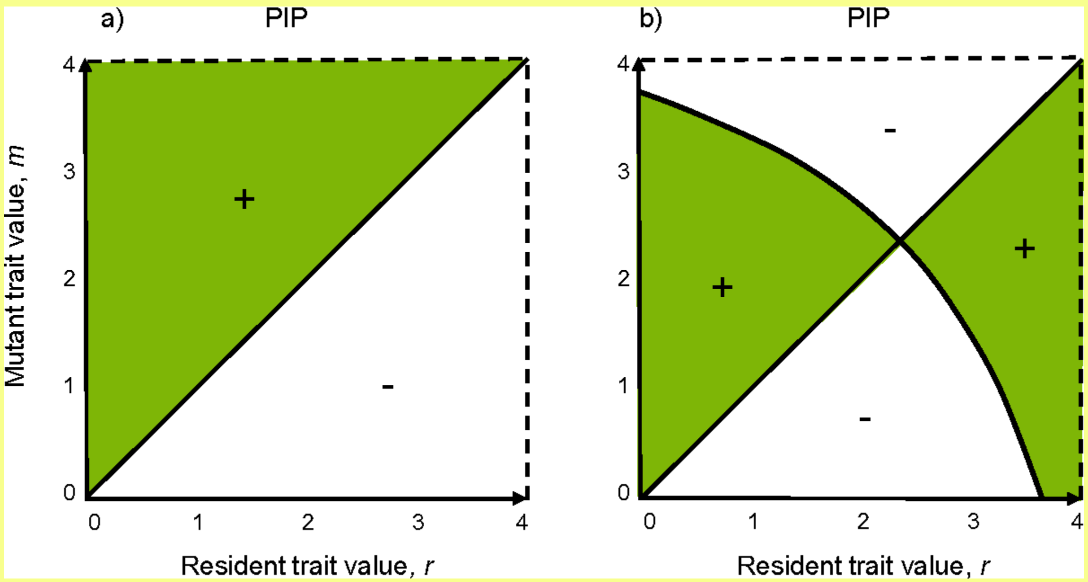
A strategy that, once established, cannot be invaded

The fitness surface is now dynamic



Evolutionary dynamics of phenotypes

- ***r(v,u) is the fitness of a rare phenotype v invading a population in which u is established***



The-Hitchhiker's-Guide-to-Adaptive-Dynamics-Brännström-Johansson//4

This leads to a powerful way to understand observed strategies

- *Begin with a basic dynamical model*
- *Allow (heritable) variation in the traits of interacting individuals*
- *Explore the adaptive dynamics of such systems, including*
  - *continuously stable strategies (convergence-stable ESSes)*
  - *evolutionary branching and possible*
  - *coexistence of types*

Life Histories

Reproductive allocation

- Survival (l_x)
- Growth (subsequent m_x)
- Current reproduction (m_x)

Shoots, roots, leaves

Dormancy (and diapause)

- Spreading reproduction—
  - bet hedging (pool)

Dispersal

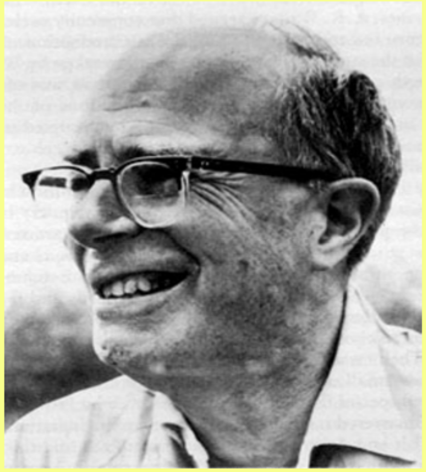
- Also spreads risks

Clutch size

Doligez and Clobert. 2003. Clutch size reduction as a response to increased nest predation rate in the Collared Flycatcher. *Ecology* 84:2582–2588

www.esapubs.org/.../ecol/ E084/066/appendix-B.htm

Theoretical approaches to clutch size: David Lack



Optimal Clutch Size

Suppose an animal can increase its litter (m_x) by 1. Should it?

Costs

1. Decrease survival of young
2. Tradeoffs between m_x *and* l_x
3. Tradeoffs between m_x and other values of l_y and m_y

Measure

1. Overall effect on λ
2. Effects on mean reproductive value

Compare

Human clutch size

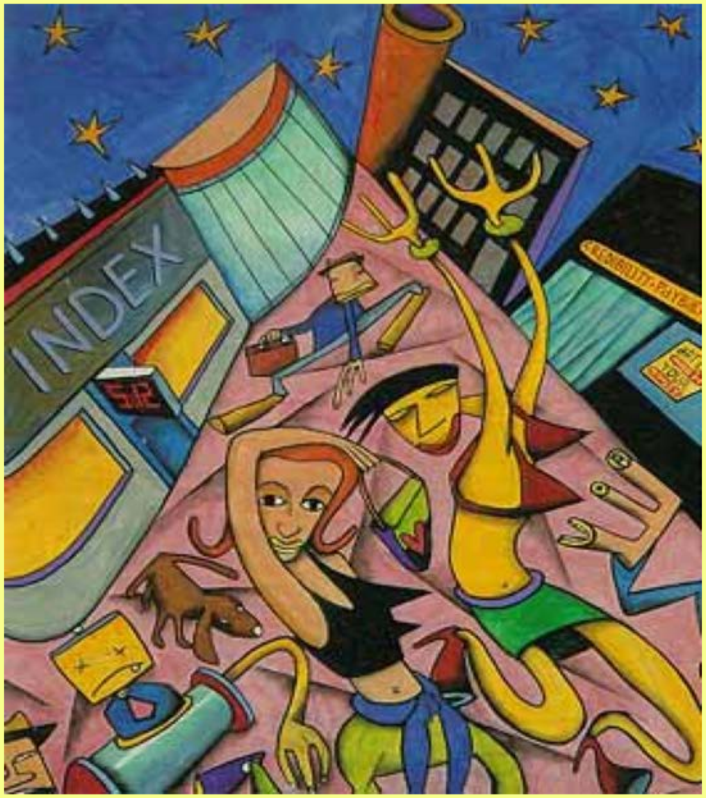
Intergenerational effects:

Offspring with more resources produce healthier offspring

Livnat, Pacala, Levin:

Idealists vs. Hedonists

keirsey.com



www.artzone.com

Livnat, Pacala, Levin:

Idealists vs. Hedonists

http://members.telering.at

- Idealists (I) produce small clutches, investing large amounts of resources in each
- Hedonists (H) produce large clutches, investing small amounts of resources in each

Discounting

- Key to how individuals and societies value the future
- Exponential discounting: Payoff P at time t is worth P exp(-rt) today
- Hyperbolic discounting: Distant future is discounted at lower rate than immediate future

Hyperbolic discounting can account for intertemporal inconsistencies in actions

www.norasco.com(ITAR-TASS