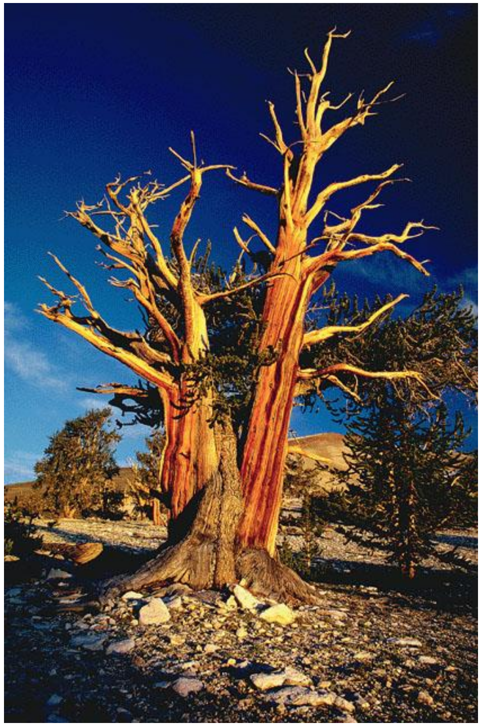
Life histories



What is a life history?

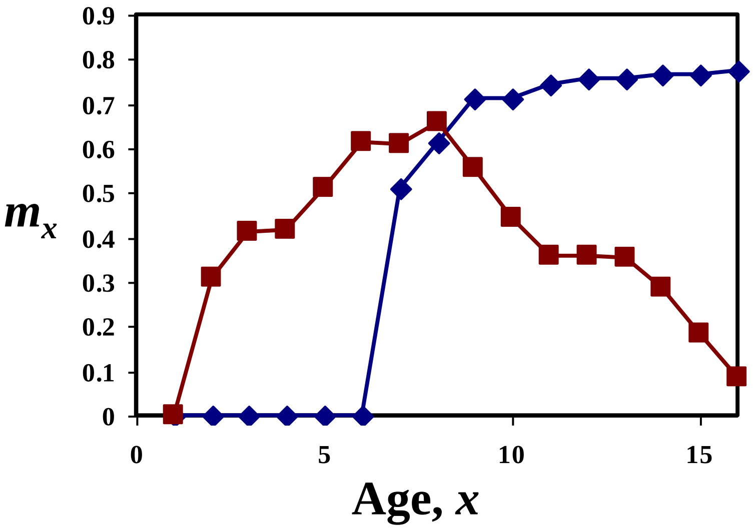
Life History – An individual's pattern of allocation, throughout life, of time and energy to various fundamental activities, such as growth, reproduction, and repair of cell and tissue damage.

Examples of life history traits

- **Size at birth**
- **Age specific reproductive investment**
- **Number, and size of offspring**
- **Age at maturity**
- **Length of life**

Age specific reproductive investment

x	l_x	m_x
1	1	0
2	.863	0
3	.778	0
4	.694	0
5	.610	0
6	.526	0
7	.442	.510
8	.357	.612
9	.181	.712
10	.059	.713
11	.051	.745
12	.042	.756
13	.034	.758
14	.025	.765
15	.017	.766
16	.009	.773



x	l_x	m_x
1	1	0
2	.863	.311
3	.778	.412
4	.694	.415
5	.610	.512
6	.526	.612
7	.442	.611
8	.357	.656
9	.181	.557
10	.059	.442
11	.051	.358
12	.042	.356
13	.034	.352
14	.025	.285
15	.017	.185
16	.009	.086

An extreme case: semalparity vs. iteroparity

Semelparous

x	l_x	m_x
1	1	0
2	.863	0
3	.778	0
4	.694	0
5	.610	0
6	.526	0
7	.442	0
8	.357	0
9	.181	0
10	.059	0
11	.051	0
12	.042	0
13	.034	0
14	.025	0
15	.017	0
16	.009	2.0

Semelparity – A life history in which individuals reproduce only once in their lifetime.

Iteroparity – A life history in which individuals reproduce more than once in their lifetime.

Iteroparous

x	l_x	m_x
1	1	.125
2	.863	.125
3	.778	.125
4	.694	.125
5	.610	.125
6	.526	.125
7	.442	.125
8	.357	.125
9	.181	.125
10	.059	.125
11	.051	.125
12	.042	.125
13	.034	.125
14	.025	.125
15	.017	.125
16	.009	.125

An example: *Oncorhyncus mykiss*

Steelhead

- **Live a portion of their life in saltwater**
- **Migrate to freshwater to spawn**
- **Often semelparous**

Rainbow trout

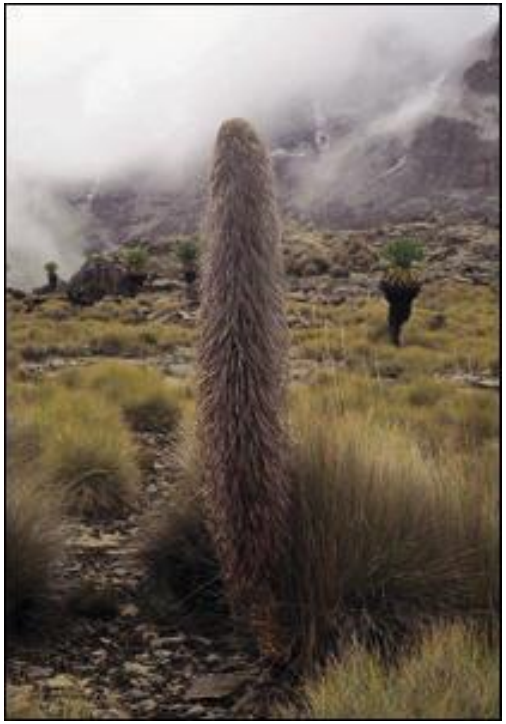
- **Spend entire life in freshwater**
- **Iteroparous**

An example: Mt Kenya *Lobelias*

***Lobelias* live on Mt Kenya from 3300-5000m!**

Mt Kenya *Lobelias*

Lobelia keniensis
(iteroparous)



Lobelia telekii
(semalparous)

Why be semalparous vs. iteroparous?

A model of annuals vs. perennials: Cole (1954)

$$N_{A,t+1} = B_A N_{A,t}$$

$$N_{P,t+1} = B_P N_{P,t} + N_{P,t} = (B_P + 1) N_{P,t}$$

B **is the # of seeds produced (assumes that all seeds survive)**

Based on these equations, when would the relative numbers of annuals and perennials not change?

Cole's Paradox

The relative abundance of annuals and perennials will not change if their *per capita growth rates* are equal:

$$B_A = B_P + 1$$

- **An annual need only produce one more seed per generation to out-reproduce a perennial. So why are there any perennials at all?**

A resolution to Cole's Paradox

Assumptions of Cole's model

- No adult mortality in the perennial
- No juvenile mortality in either the annual or the perennial

Relaxing these assumptions: Charnov and Schaffer (1973)

- Adults survive each year with probability P_a
- Juveniles survive to adulthood with probability P_j

A resolution to Cole's Paradox

$$N_{A,t+1} = P_j B_A N_{A,t}$$

$$N_{P,t+1} = P_j B_P N_{P,t} + P_a N_{P,t} = (P_j B_P + P_a) N_{P,t}$$

A resolution to Cole's Paradox

The relative abundance of annuals and perennials will not change if their *per capita growth rates* are equal:

$$P_j B_A = P_j B_P + P_a$$

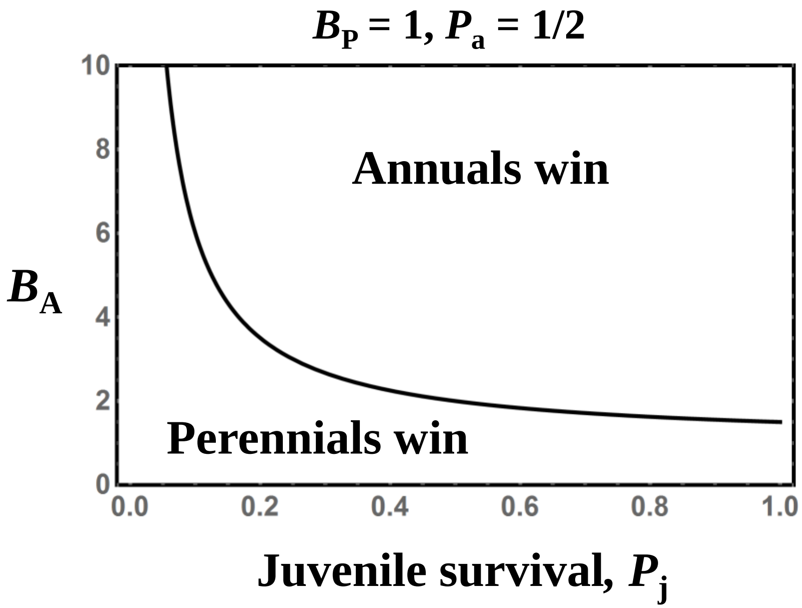
Which after a little algebra is:

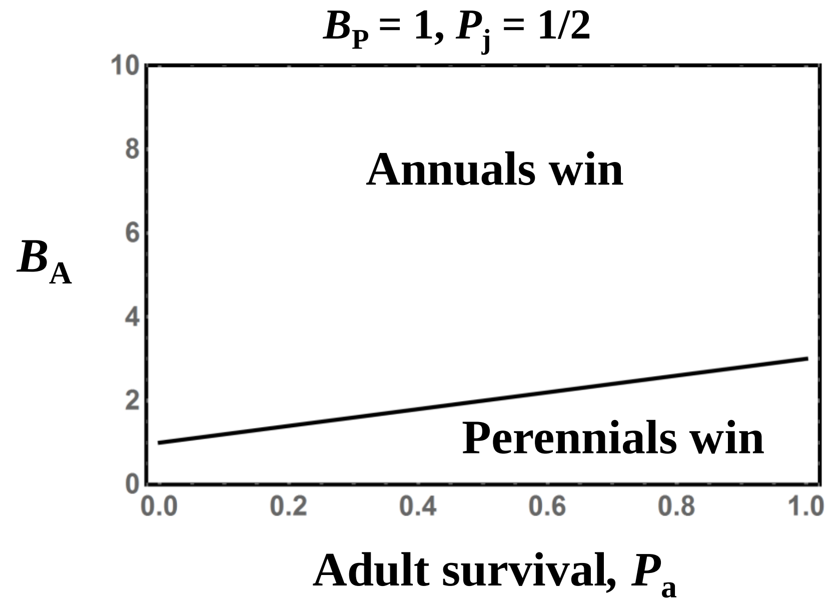
$$B_A = B_P + \frac{P_a}{P_j}$$

- **Annuals (semalaparity) are favored by low adult survival and high juvenile survival**

- **Perennials (iteroparity) are favored by high adult survival and low juvenile survival**

A resolution to Cole's Paradox



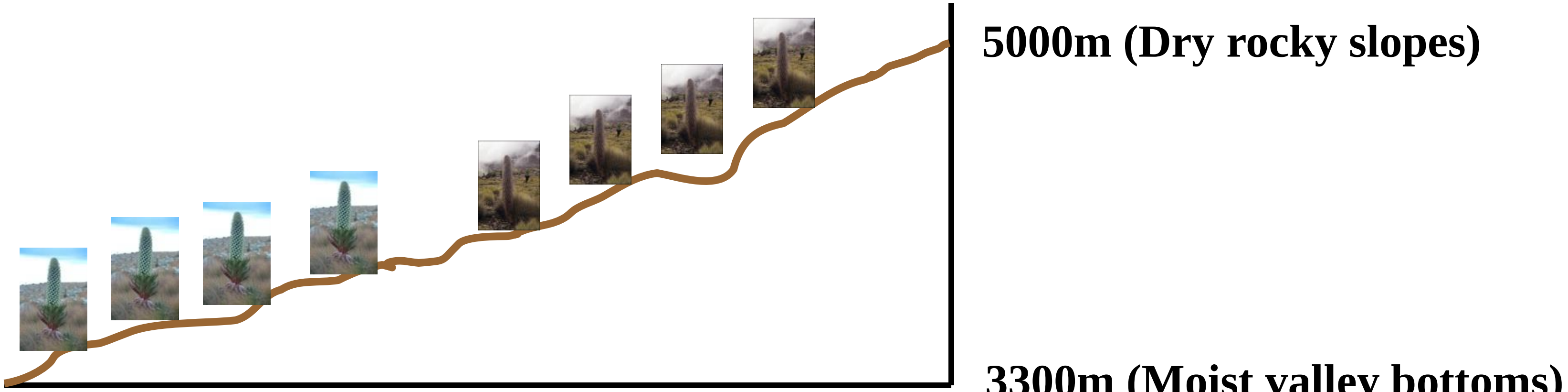


- **High rates of juvenile survival favor the evolution of annuals/semalparity**
- **High rates of adult survival favor the evolution of perennials/iteroparity**

A test of the theory: Mt Kenya *Lobelias*

Lobelia keniensis
(iteroparous)

Lobelia telekii
(semalparous)



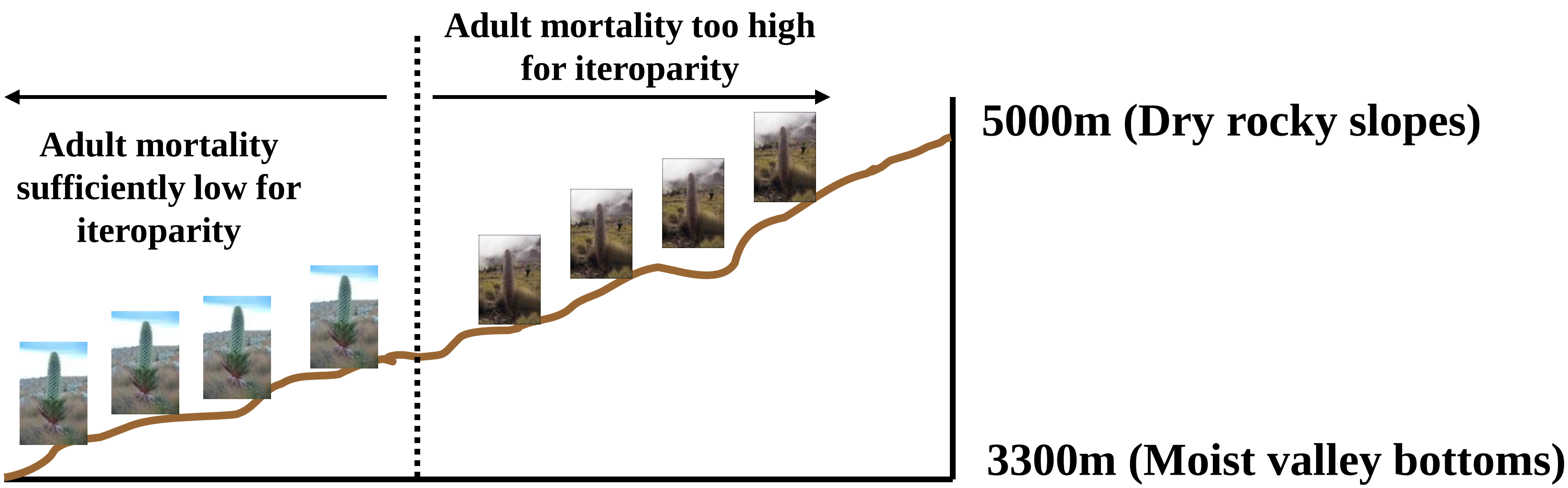
A test of the theory: Mt Kenya *Lobelias*

Young (1990)

- **Measured adult survival rates of the iteroparous species, *Lobelia keniensis*, at various sites along this environmental gradient**

- **Found that adult survival decreases as elevation increases and moisture decreases**

- **Found that the species transition zone occurs where adult survival falls below the critical threshold predicted by the model**



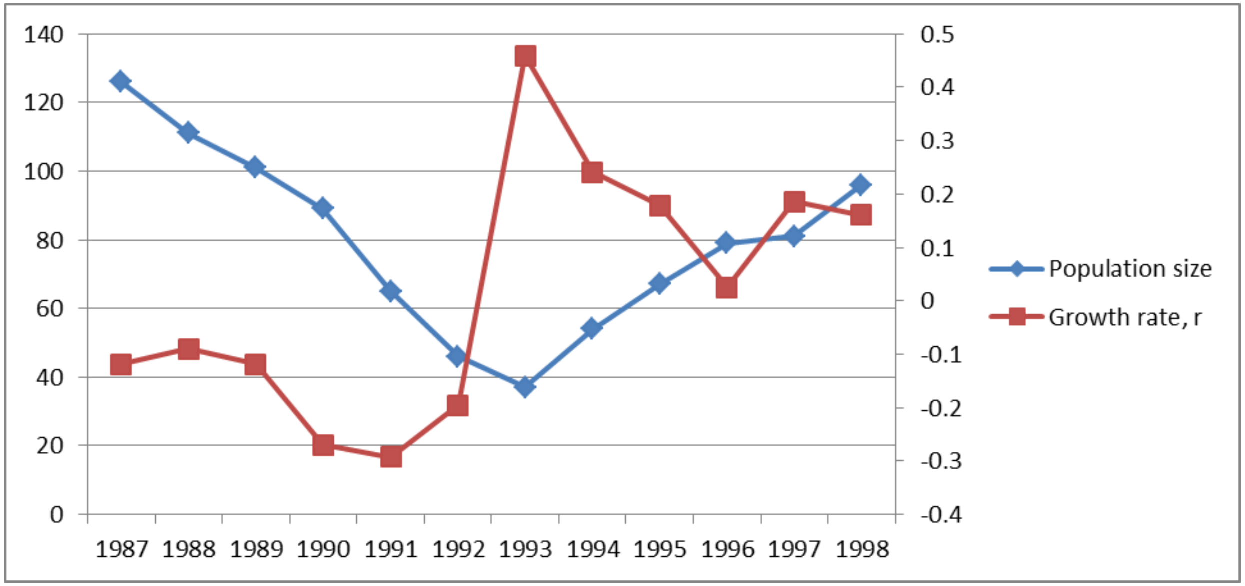
-Practice question

-In order to identify the importance of density regulation in a population of wild tigers, you assembled a data set drawn from a single population for which the population size and growth rate are known over a ten year period. This data is shown below. Does this data suggest population growth in this tiger population is density dependent? Why or why not?

Year	Population size	Growth rate, r
1987	126	-0.11905
1988	111	-0.09009
1989	101	-0.11881
1990	89	-0.26966
1991	65	-0.29231
1992	46	-0.19565
1993	37	0.459459
1994	54	0.240741
1995	67	0.179104
1996	79	0.025316
1997	81	0.185185
1998	96	0.16

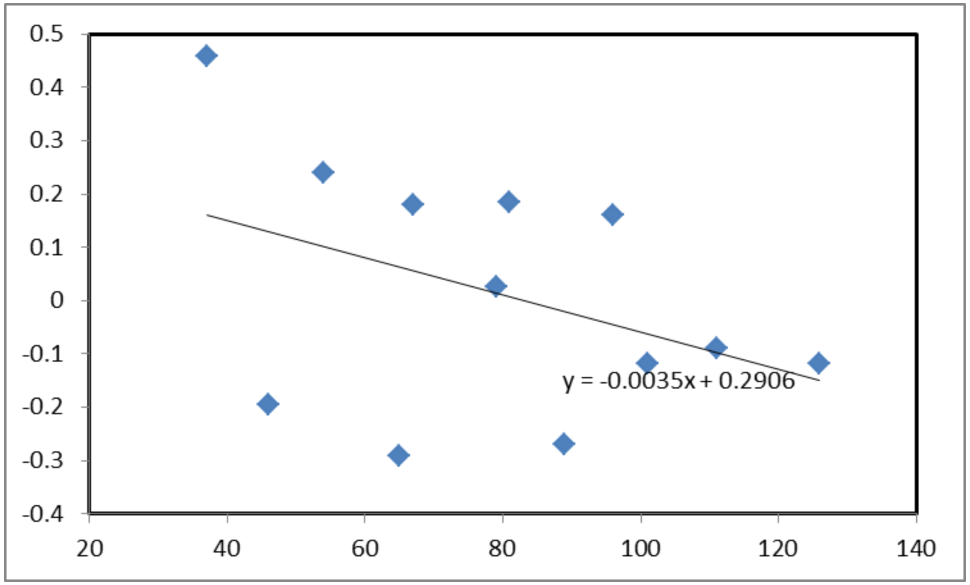
-What problems do you see with using this data to draw conclusions about density dependence?

Population size



Year

Growth rate

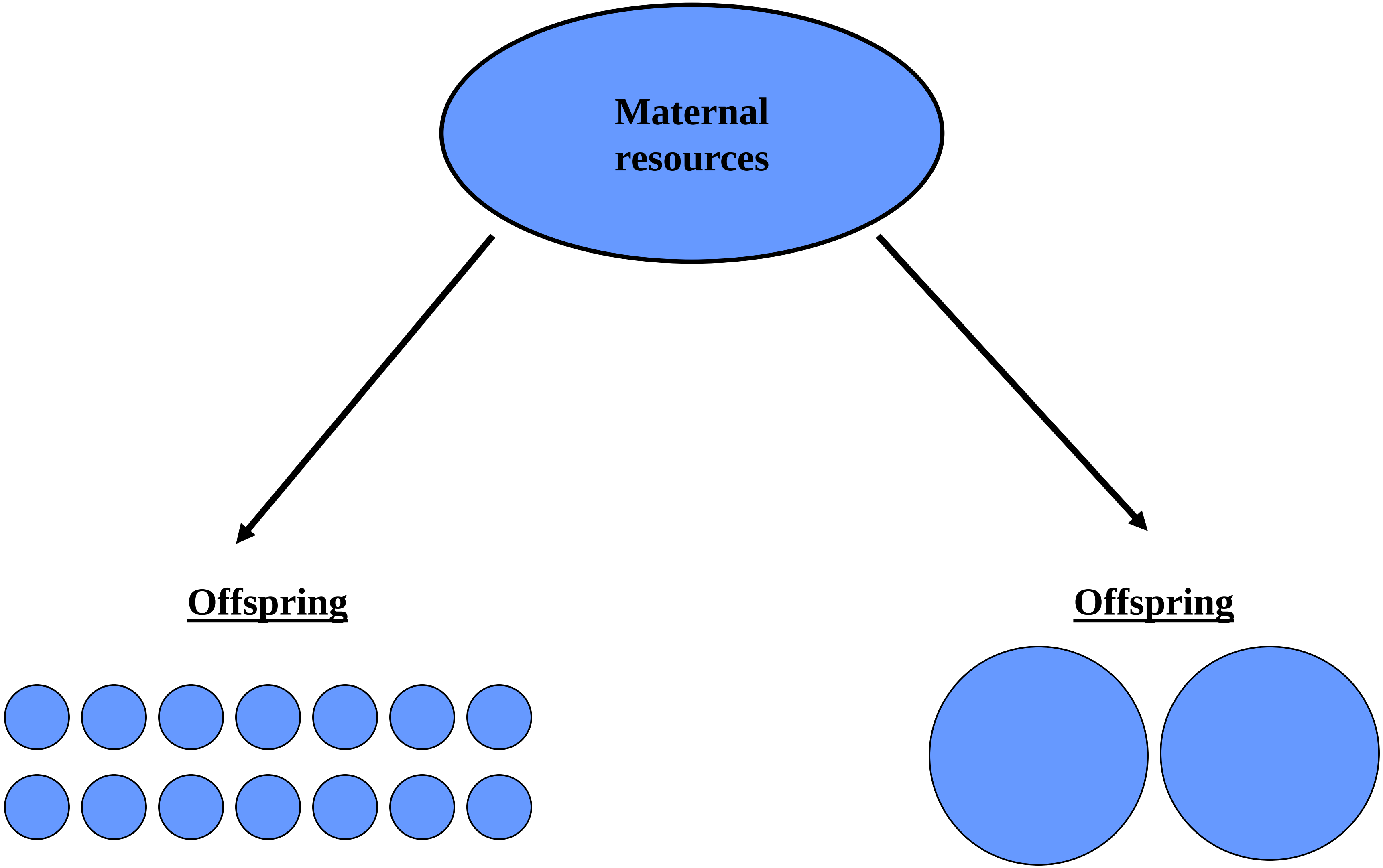


Population size

Number and size of offspring

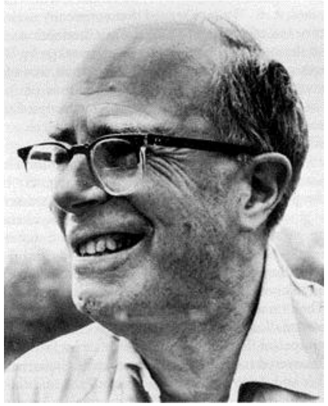
All else being equal it should be best to maximize the number of surviving offspring

A fundamental question



What is the best solution?

The Lack Clutch – The best solution is the one that maximizes the number of offspring surviving to maturity. Lack (1947)

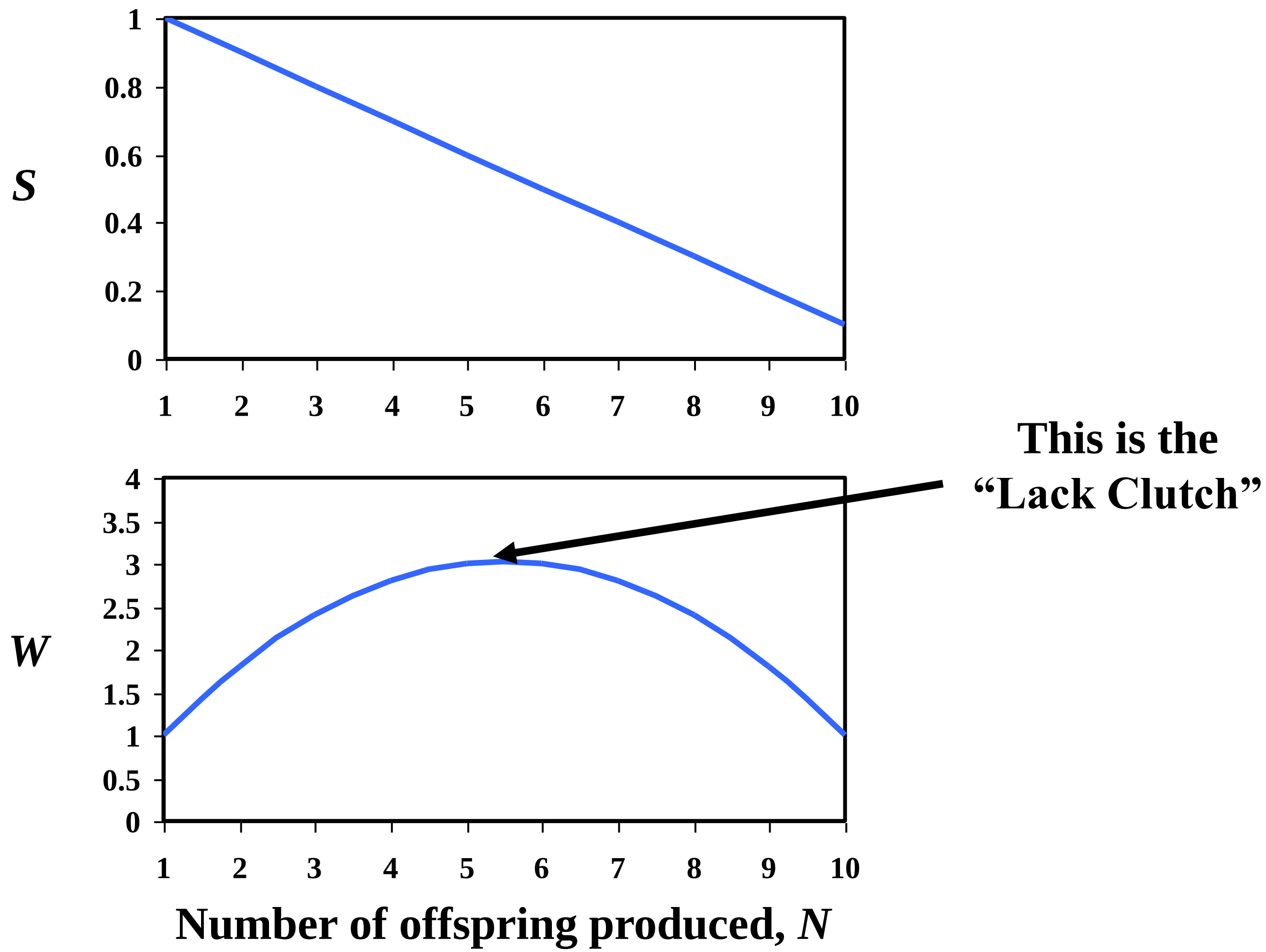


David Lack

$$W = S*N$$

There is a fundamental trade-off

$W = N*S(N)$



An example with #’s

N	*S*	*W*
2	**1**	**?**
4	**.75**	**?**
6	**.5**	**?**
8	**.25**	**?**
10	**.1**	**?**

What is the optimal number of offspring to produce in this example?

An example with #'s

N	*S*	*W*
2	1	2
4	.75	3
6	.5	3
8	.25	2
10	.1	1

What is the optimal number of offspring to produce in this example?

Do real data conform to the 'Lack Clutch'?

Table 7.2 A summary of the clutch size studies listed in Table 7.1. Effects refer to increases in clutch or brood sizes. In many cases, clutch or brood sizes were also decreased

	Number of studies		Effect of increase			
Trait	Reported	Not reported	+	−	0	% negative
Offspring						
N_f = number fledged	53	2	40	7	6	
M_f = weight of fledglings	40	15	0	27	13	68
S_0 = survival in nest	44	11	0	28	16	64
S_f = survival to next season	15	40	0	8	7	53
B_0 = future reproduction	3	52	0	3	0	100
Parents						
M_p = weight of parents	17	38	0	7	10	41
S_p = survival to next season	14	41	0	5	9	36
B_p = future reproduction	14	41	0	8	6	57

The observed clutch sizes appear consistently smaller than the 'Lack Clutch'

Table from Stearns, 1992

Where does the 'Lack Clutch' go wrong?

<u>Assumptions of the 'Lack Clutch'</u>

1. **No trade-off between clutch size and maternal mortality**

2. **No trade-off between clutch size across years**

3. **No parent-offspring conflict (who controls clutch size anyway?)**

All have been shown to be important in some real cases!

For your current research position with the USFS, you have been tasked with developing a strategy for eliminating the invasive plant, *Centaurea solstitialis*. Because you have recognized that this plant appears to thrive when it is able to attract a large number of pollinators, you are hoping that you may be able to capitalize on Allee effects to drive invasive populations to extinction. Specifically, your idea is that if you can reduce the population size of this plant below some critical threshold with herbicide treatment, Allee effects will take over and lead to extinction. In order to evaluate the feasibility of your strategy, you have conducted controlled experiments where you estimate the growth rate, r, of experimental populations of this plant when grown at different densities. Your data is shown in the table below:

Density (plants/m^2)	Growth rate (r)
35	0.46
30	0.32
25	0.24
20	0.15
15	0.08
10	0.01
5	-0.05

A. Does your data suggest Allee effects operate in this system? Justify your response

B. Additional studies conducted by others have demonstrated that herbicide application can reduce the population density of this plant, but never to densities below 17 plants/m^2. Will your strategy for controlling this invasive plant work or not? Justify your response.

Life history strategies: *r* vs. *K* selection

In the 1960's interest in life histories was stimulated by the identification of two broad classes of life history STRATEGIES (MacArthur and Wilson, 1967):

<u>*r* selected</u>

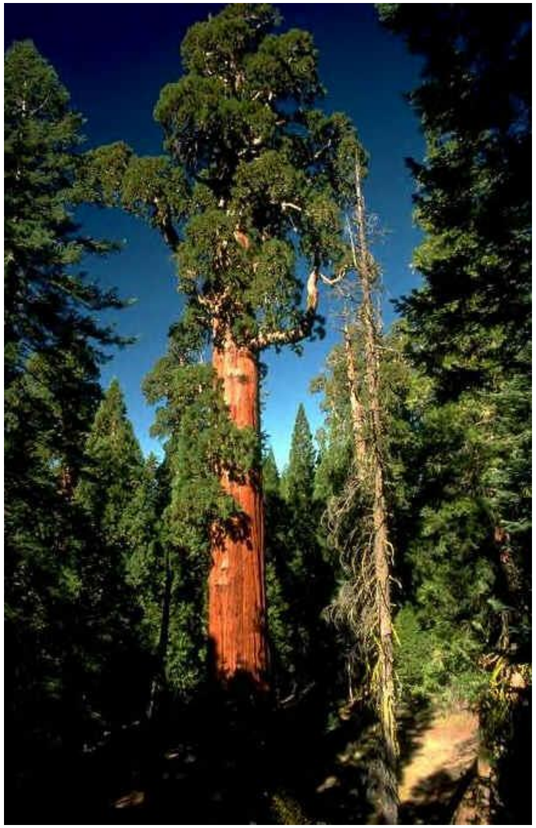
- **Mature early**
- **Have many small offspring**
- **Make a a few large reproductive efforts**
- **Die young**

<u>*K* selected</u>

- **Mature later**
- **Have few large offspring**
- **Make many small reproductive efforts**
- **Live a long time**

Putative examples of *r* vs. *K* selected species

Taraxacum officinale
Dandelion



Sequoiadendron giganteum
Redwood

Putative examples of *r* vs. *K* selected species

Peromyscus leucopus
Deer mouse

Gopherus agassizii
Desert tortoise

What conditions favor *r* vs *K* species?

A simple model of density-dependent natural selection can help (Roughgarden, 1971)

$$\Delta N = rN[1 - \frac{N}{K}]$$

of this, each INDIVIDUAL contributes:

$$\Delta N = r[1 - \frac{N}{K}]$$

to population growth

A simple model of density dependent selection

Since an individual's contribution to population growth is intimately connected to the notion of individual fitness, Roughgarden assumed the fitness of various genotypes is:

$$W_{AA} = 1 + r_{AA}(1 - \frac{N}{K_{AA}})$$

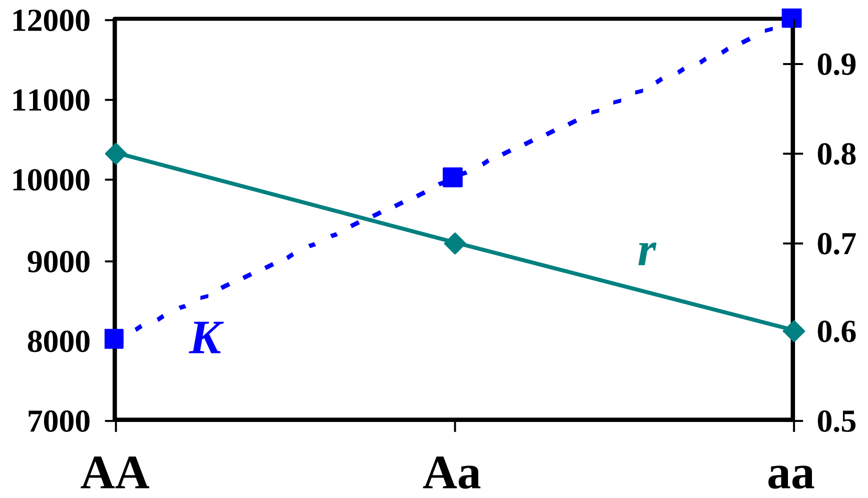
$$W_{Aa} = 1 + r_{Aa}(1 - \frac{N}{K_{Aa}})$$

$$W_{aa} = 1 + r_{aa}(1 - \frac{N}{K_{aa}})$$

Roughgarden (1971)

A critical assumption

There is an inherent trade-off between '*K*' and '*r*'



Genotypes with a large '*r*' value tend to have a small '*K*' value

Can an allele that increases *r* but decreases *K* fix?

Example 1:

$r_{AA} = .15 \quad K_{AA} = 900$

$r_{Aa} = .10 \quad K_{Aa} = 950$

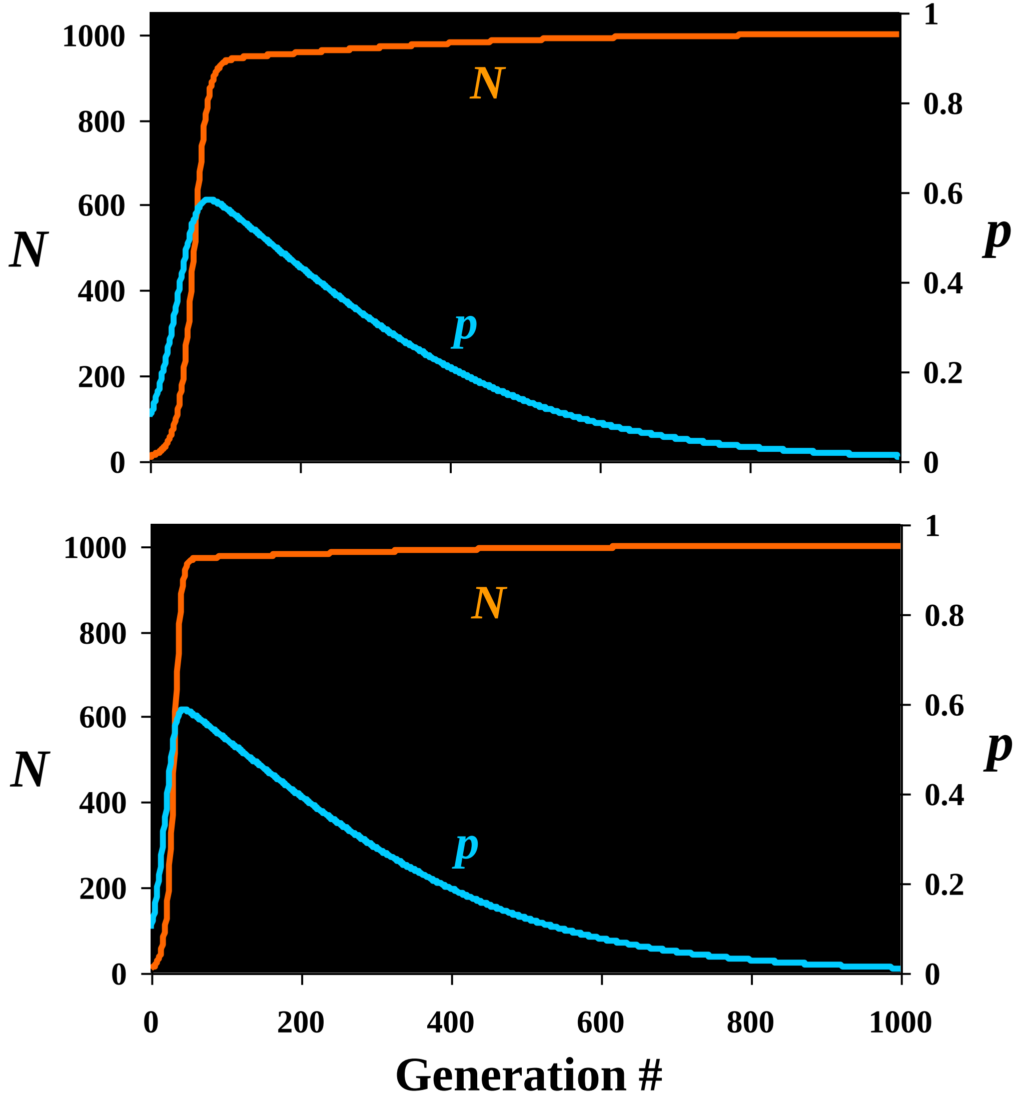
$r_{aa} = .05 \quad K_{aa} = 1000$

Example 2:

$r_{AA} = .30 \quad K_{AA} = 950$

$r_{Aa} = .20 \quad K_{Aa} = 975$

$r_{aa} = .10 \quad K_{aa} = 1000$



In a constant environment, NO!

Why does the *‘r’* selected genotype lose?

- **In a constant environment the population will ultimately approach its carrying capacity**

- **As the population size approaches the carrying capacity of the various genotypes, density dependent selection becomes strong**

- **Under these conditions, genotypes with a high ‘*K*’ are favored by natural selection**

What about 'disturbed' environments?

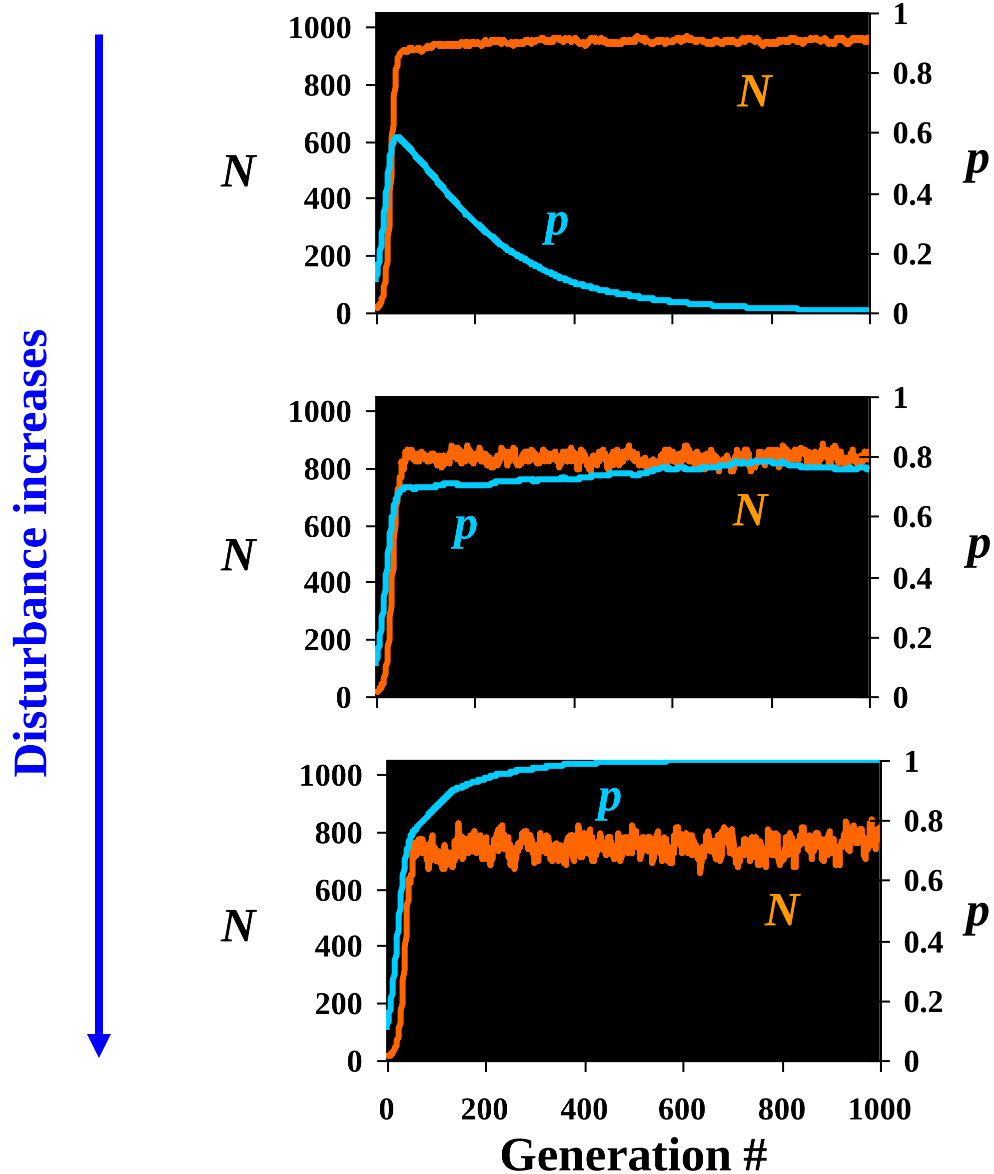
In the examples at right, the population size is reduced (disturbed) by a random amount in each generation.

<u>In this example:</u>

$r_{AA} = .30$ $K_{AA} = 900$

$r_{Aa} = .20$ $K_{Aa} = 950$

$r_{aa} = .10$ $K_{aa} = 1000$



Conclusions for *‘r’* and *‘K’* selection

• **In a constant environment the population will ultimately approach its carrying capacity and the genotype with the highest ‘*K*’ will become fixed**

• **If population size remains sufficiently below the ‘*K*’s of the various genotypes due to random environmental disturbances or other factors, the genotype with the highest *‘r’* will become fixed in the population**

A test of ‘*r*’ vs. ‘*K*’ selection:

Dandelions and disturbance (Solbrig, 1971)

- Four genotypes A-D.
  - Genotype ‘A’ has the largest allocation to rapid seed production
  - Genotype ‘D’ delays reproduction until after substantial leaf formation
  - Genotypes ‘B’ and ‘C’ are intermediate

- Established three plots with varying levels of disturbance
  - Heavily disturbed by weekly lawn mowing
  - Moderately disturbed with monthly lawn mowing
  - Minimal disturbance with seasonal lawn mowing

Dandelions and disturbance (Solbrig, 1971)

"*r* selected" genotype → A

"*K* selected" genotype → D

Disturbance level	A Early Reproduction	B	C	D Late Reproduction
High	73	13	14	0
Medium	53	32	14	1
Low	17	8	11	64

- High levels of disturbance favored the genotype with the greatest *r*