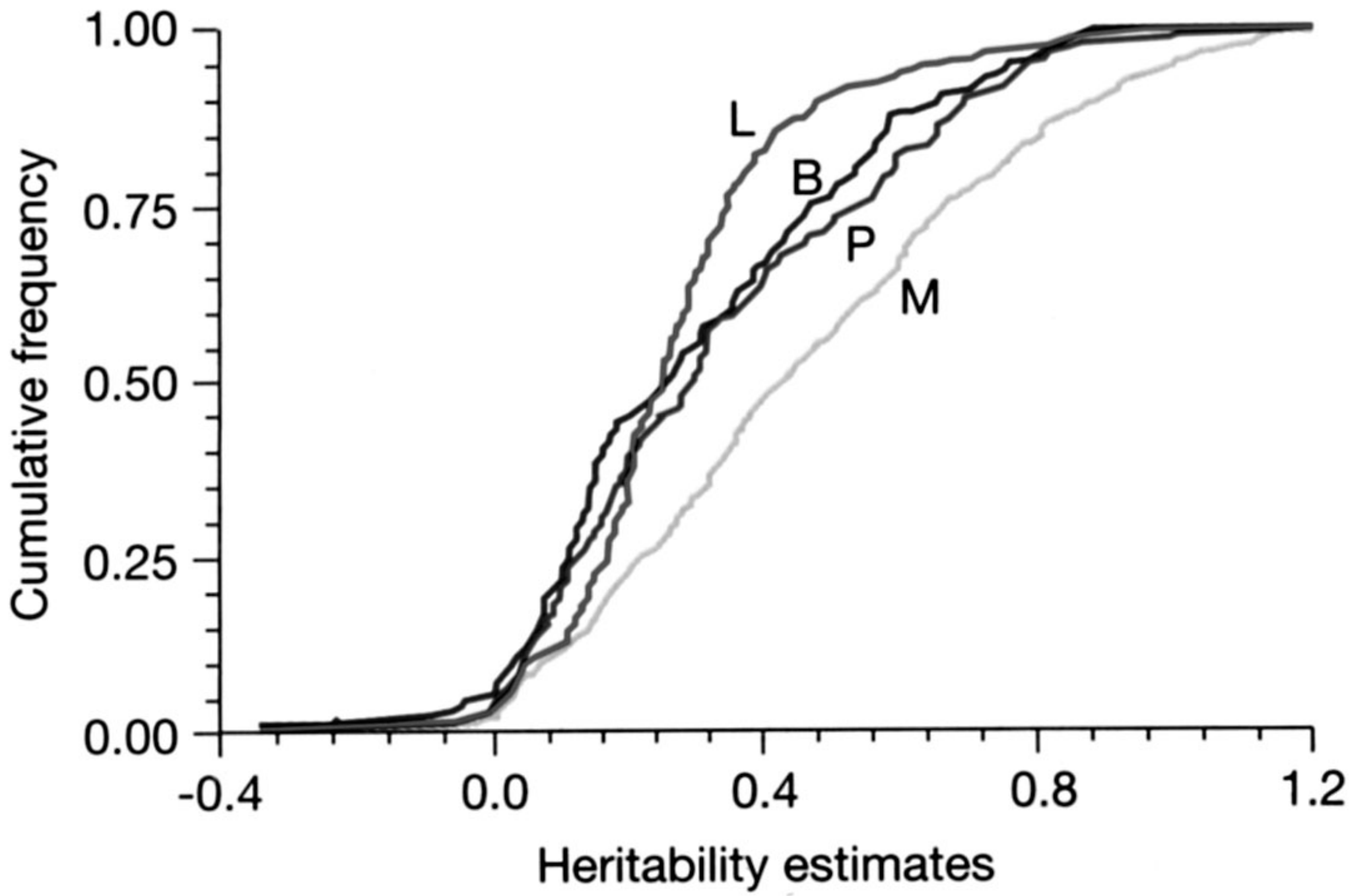
Life History Evolution

- Introduction
  - Life history traits
  - Life table
- Size and number of offspring
  - Offspring number
  - Offspring size
- Senescence

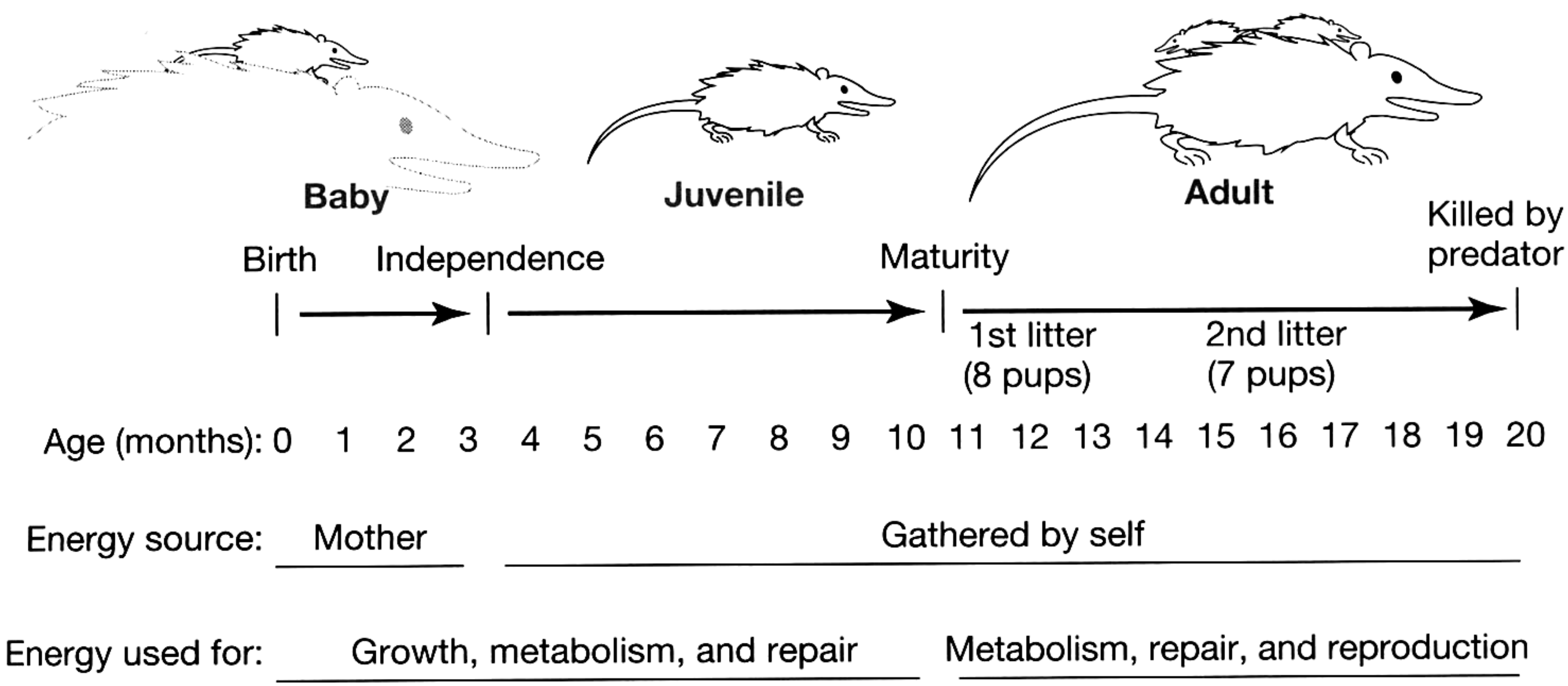
Life history traits: traits closely related to reproduction

- Age at sexual maturity
- Size at maturity
- Number of offspring produced
- Size of offspring produced
- Number of reproductive episodes
  - Semelparous
  - Iteroparous

Tend to have low (but significant) genetic variation



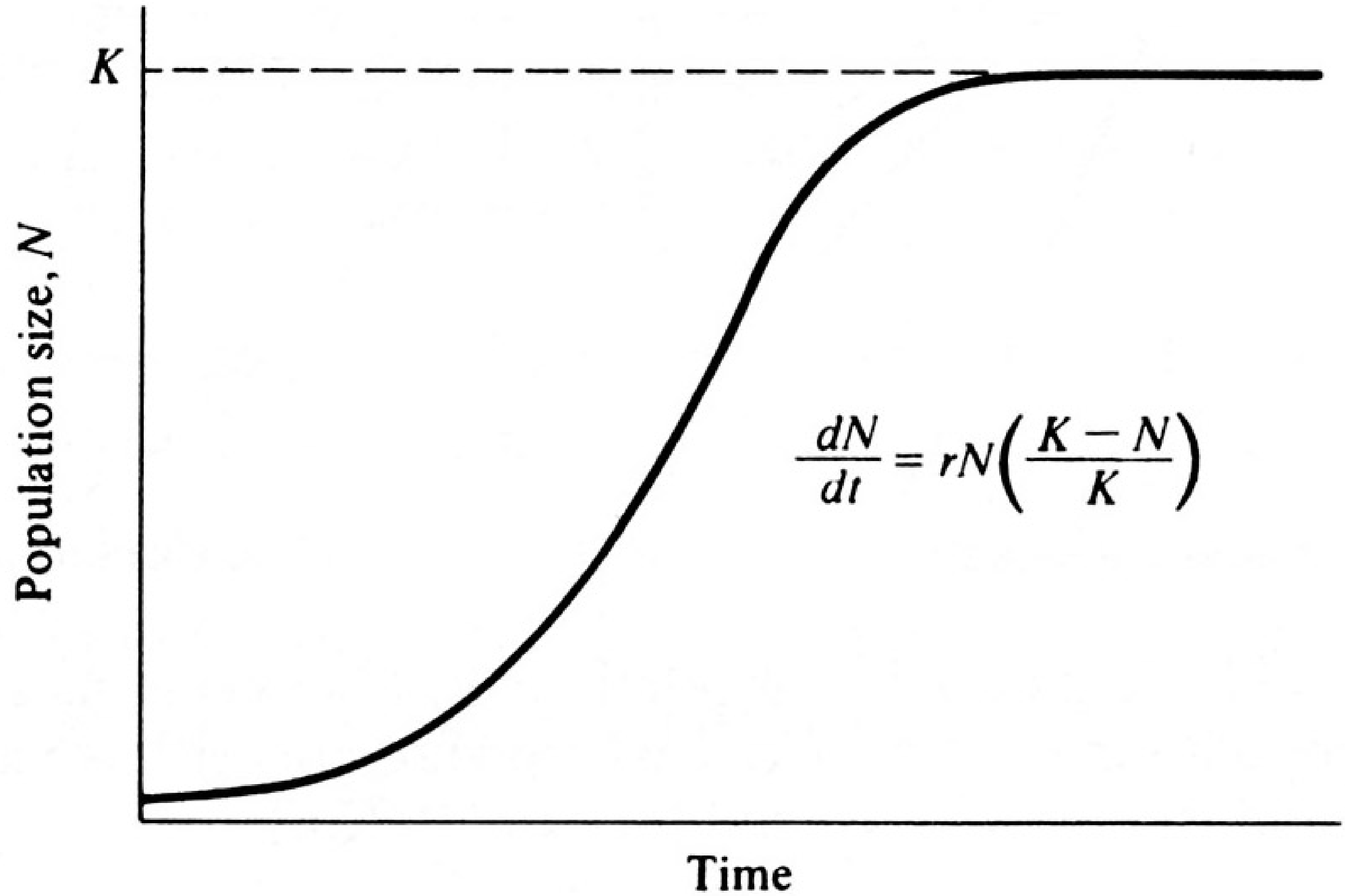
Energy acquisition and allocation



Life table

Age	lx	mx	lxmx
0	1	0	0
1	.8	0	0
2	.64	0	0
3	.512	1	.512
4	.410	1	.410
5	.328	1	.328
6	.262	1	.262
7	.210	1	.210
8	.168	0	0
		Ro =	1.722

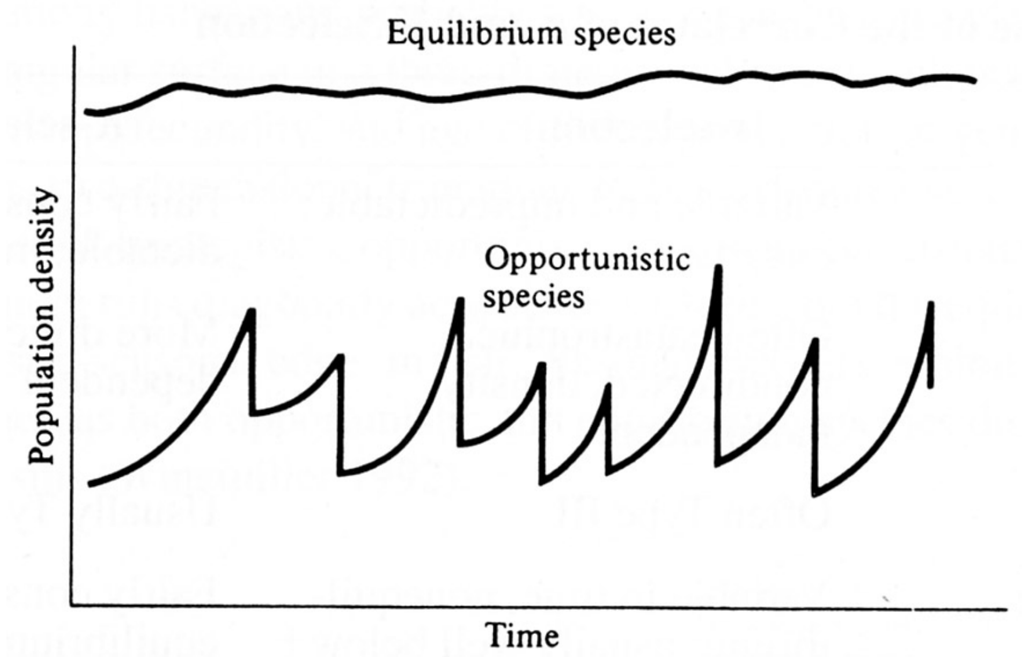
Population growth



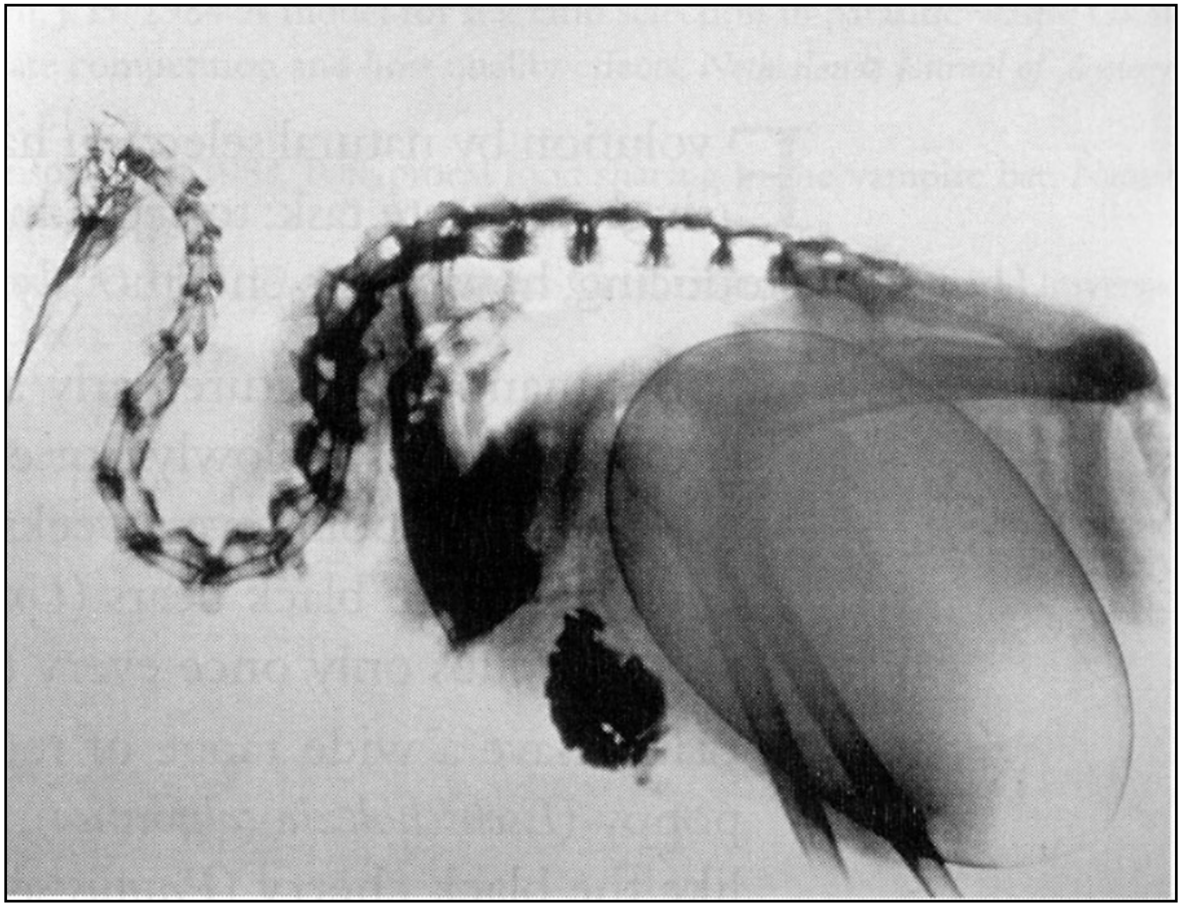
r = potential reproductive rate; K = carrying capacity

r and K selection

- R selected species
  - Many small offspring, high reproductive potential
- K selected species
  - Fewer larger offspring, high competitive potential

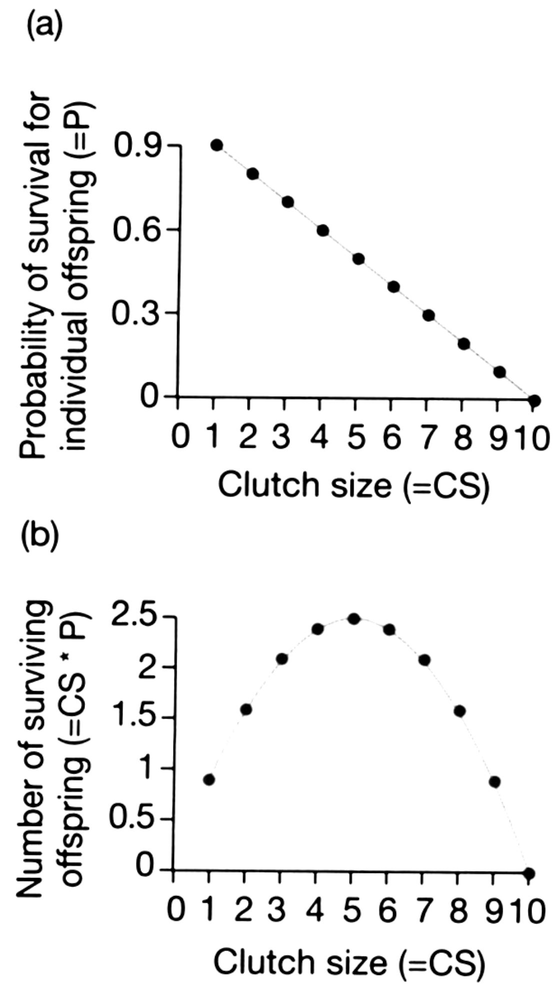


Allocation of reproductive resources



Offspring size and number

- Trade-off
  - More smaller kids, or fewer larger kids
  - More kids lower chance of survival for each kid
- Optimum clutch size
  - Number of kids that maximizes RS

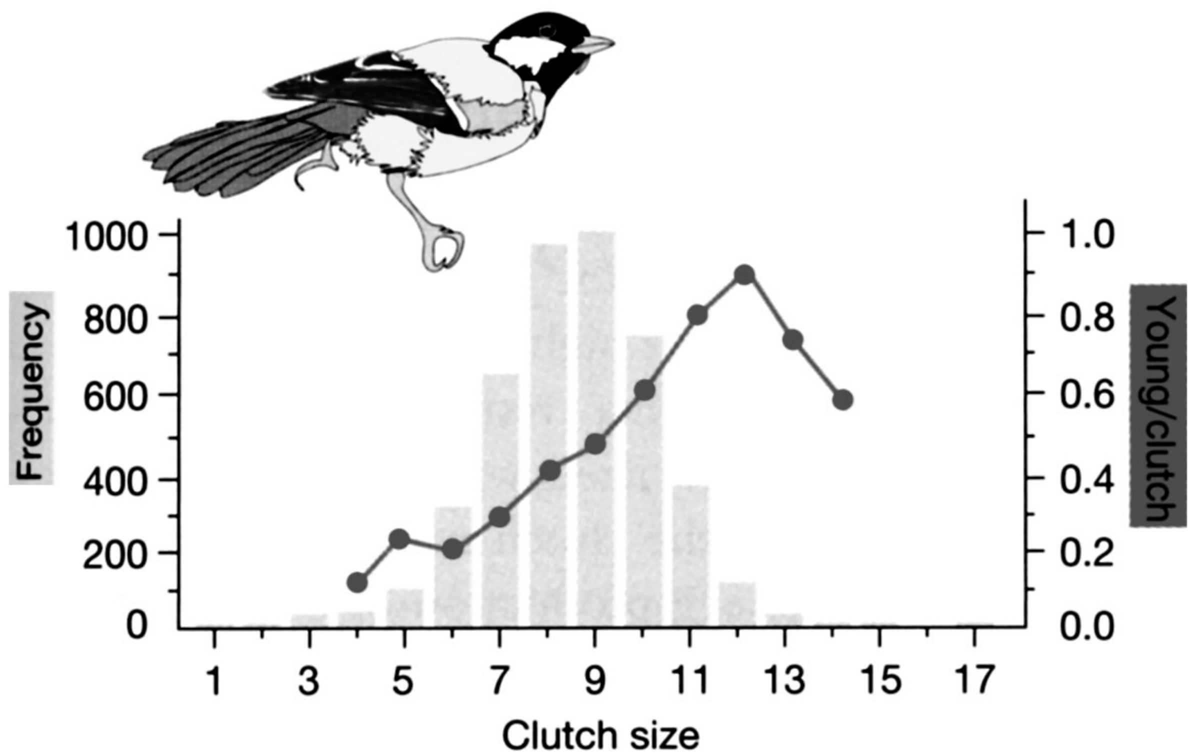


Lack’s hypothesis

- Organisms lay optimal clutch size to maximize their RS
- Bird clutch size well studied
  - Add eggs, remove eggs, count eggs
- Typical results are that birds lay too few eggs!!

Great tits *Parus major*

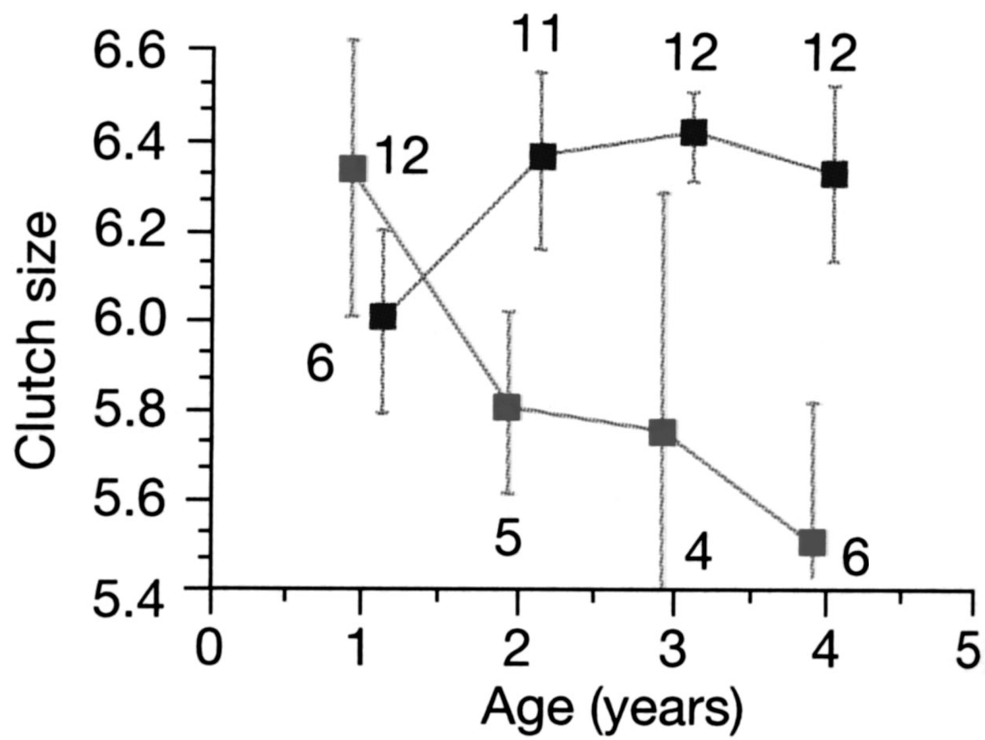
- Observed average clutch size of about 9
- Highest fitness with clutch size about 12!



So why sub-optimal clutch sizes?

- Organisms maximize their *lifetime RS*
  - Trade-off b/w current and future reproduction
  - Trade-off b/w current reproduction and future survival

Collared flycatchers. Red boxes had experimentally increased clutch size year 1.



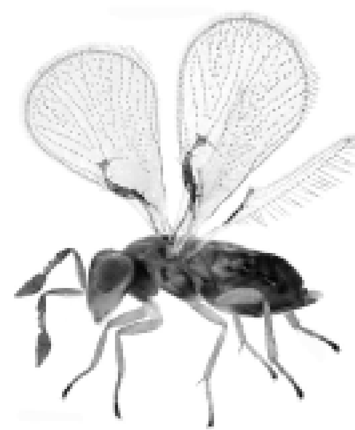
Trade-off of time and reproduction

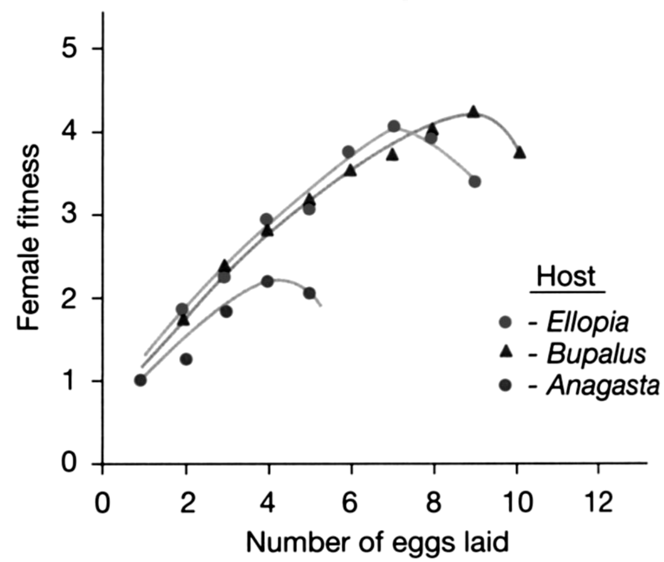
Trichogramma parasitoid wasps

Among the smallest of insects, adult size often less than 1 mm.

Lay eggs in the eggs of other insects.

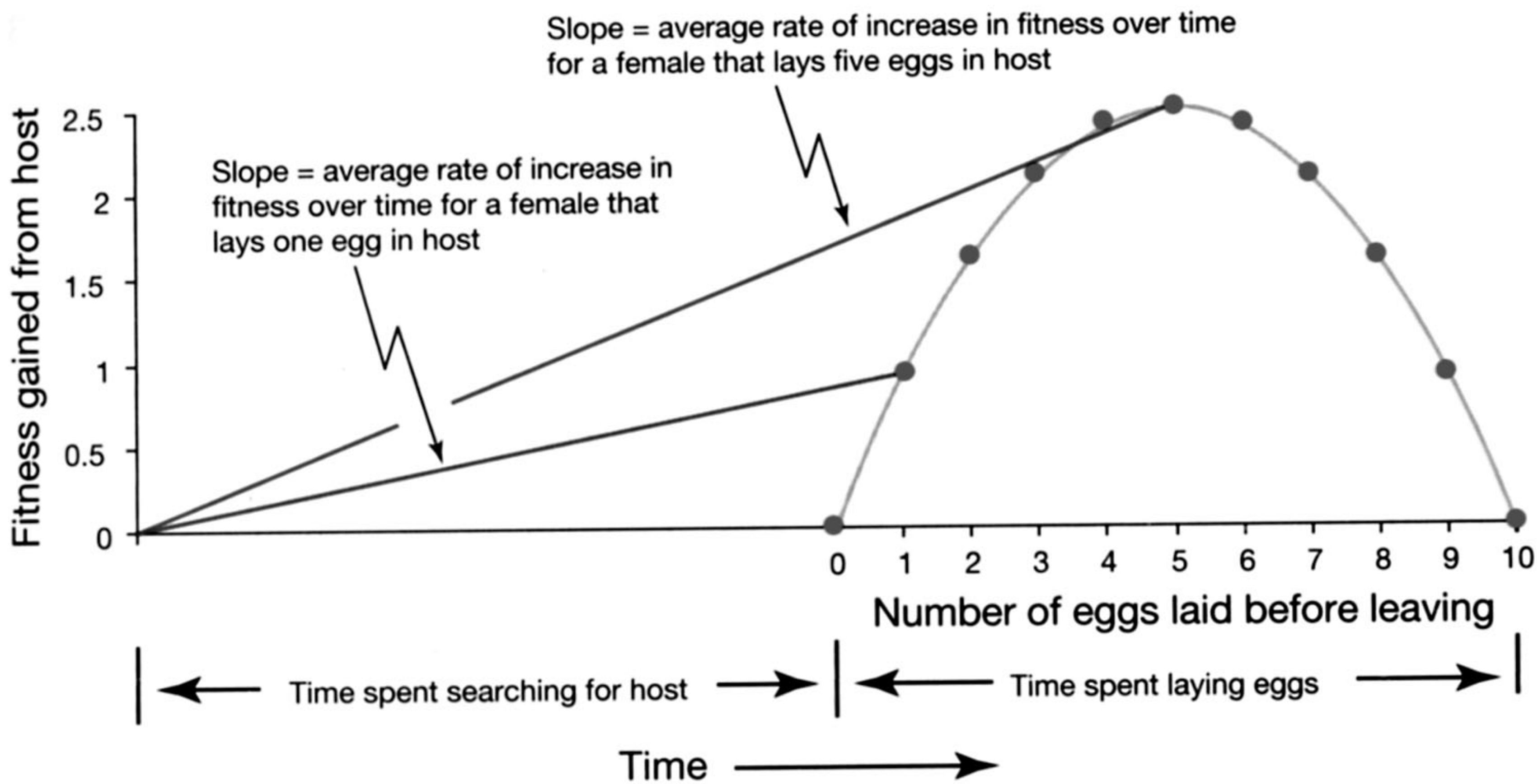
Lay more eggs in better hosts.





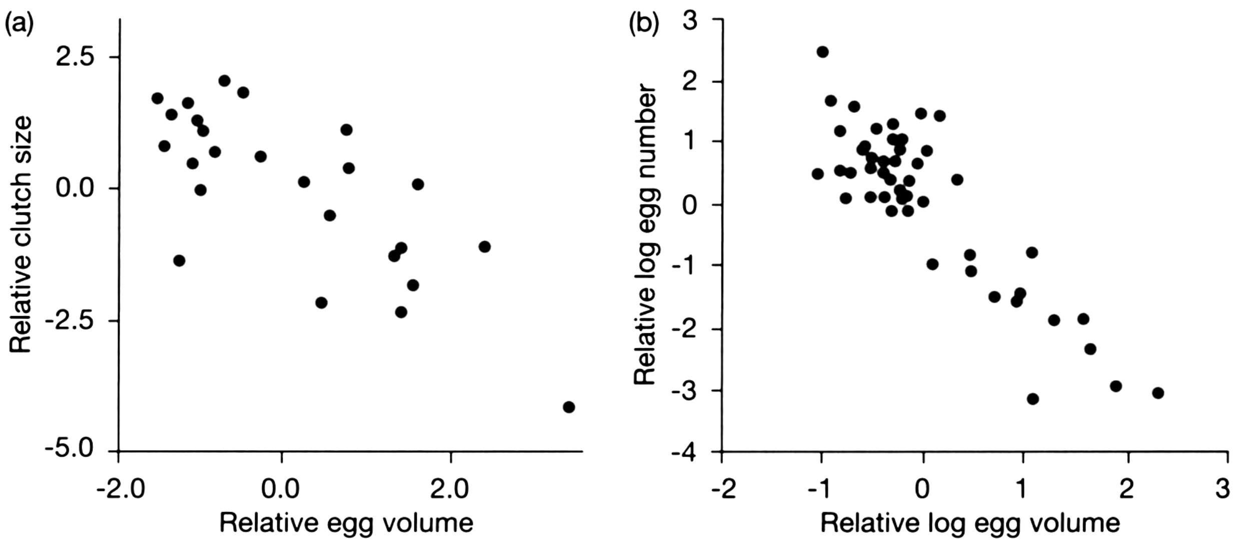
Optimal number of eggs to lay:

depends on travel time to find new host



How big should offspring be?

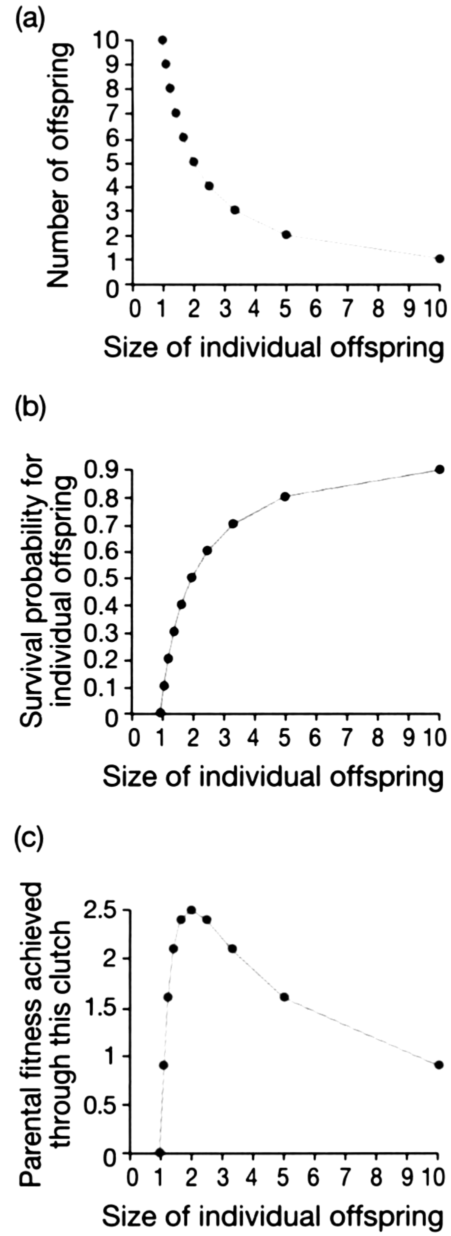
- Trade-off of size and number



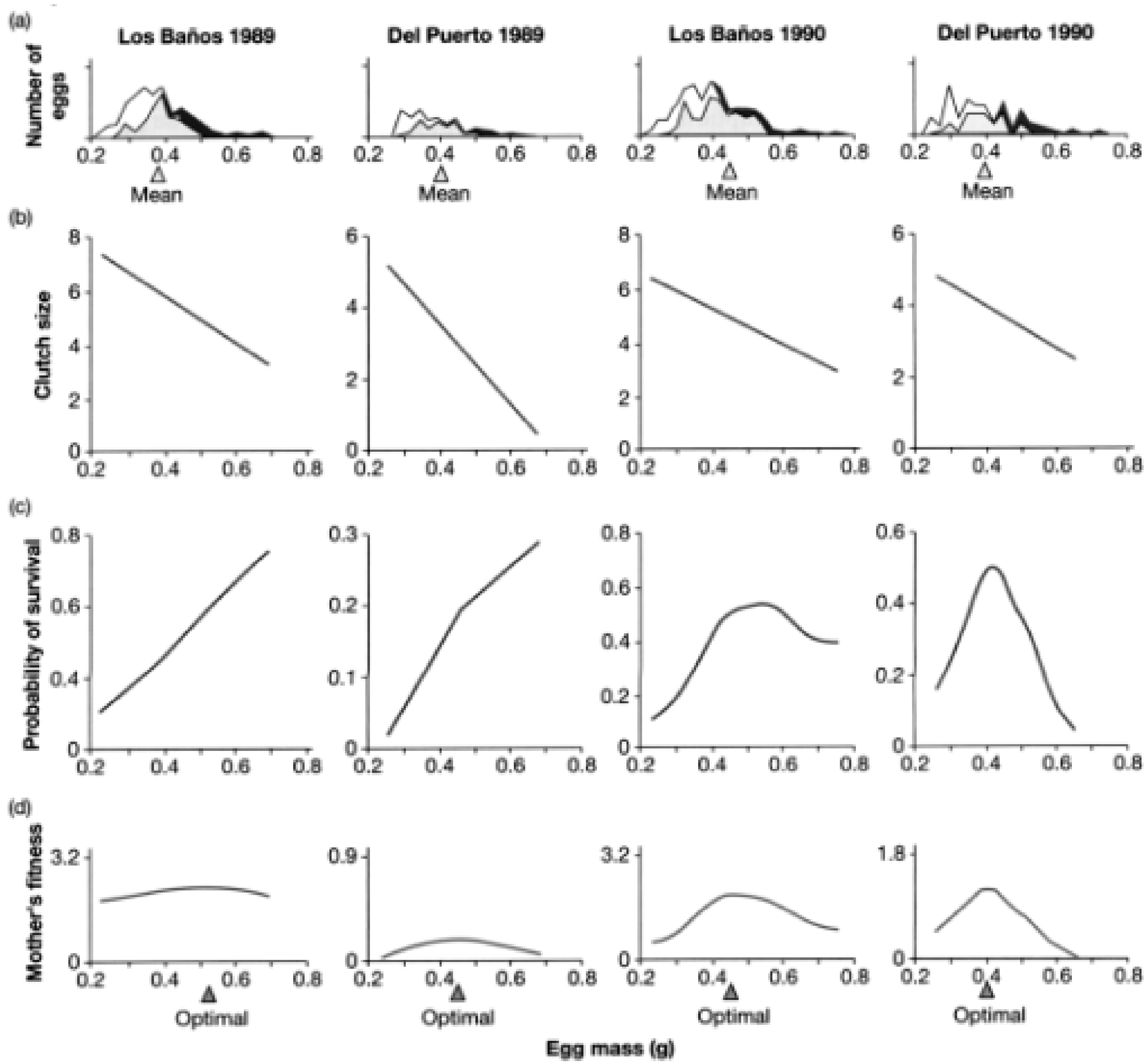
26 Fish species Fruit fly species

Smith-Fretwell model

- Two assumptions only
- Trade-off between size and number
- Larger offspring more likely to survive
- Optimal size from parent's point of view often less than from offspring's perspective



Lizard egg size

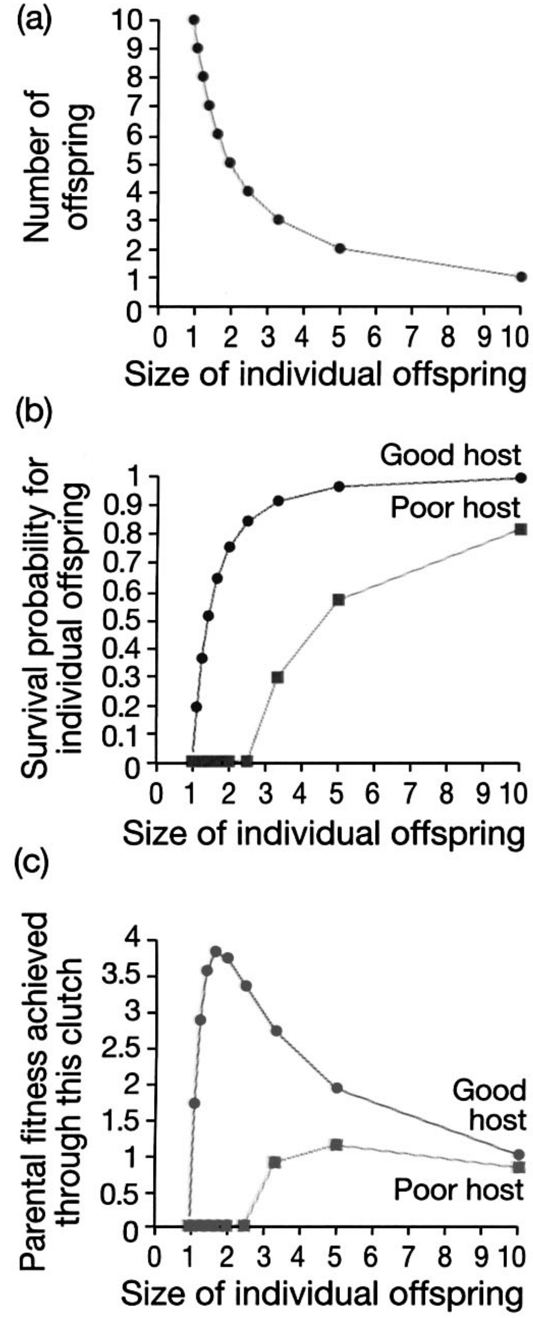


Stator limbatus
Seed beetle (Bruchidae)

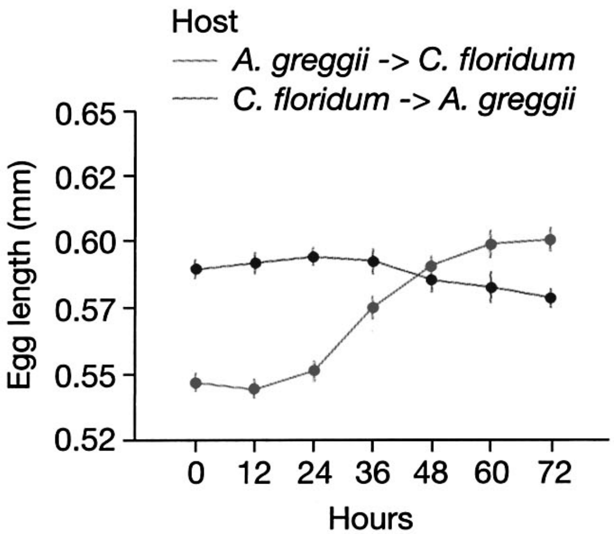
Generalist: offspring reared from seeds of over 50 host plants

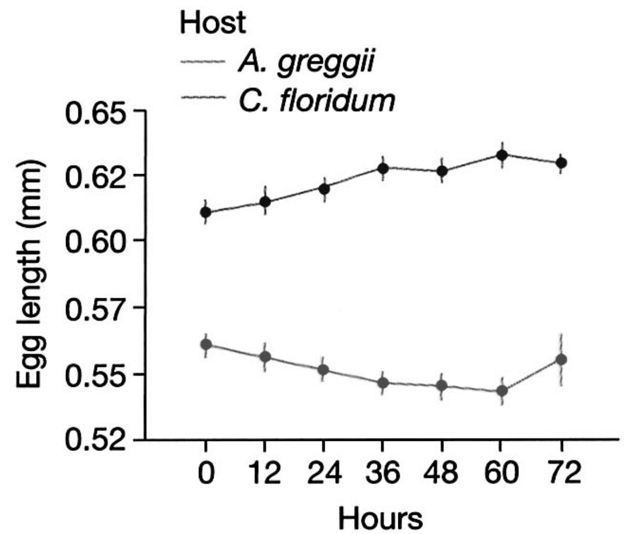
Variation in host seed quality

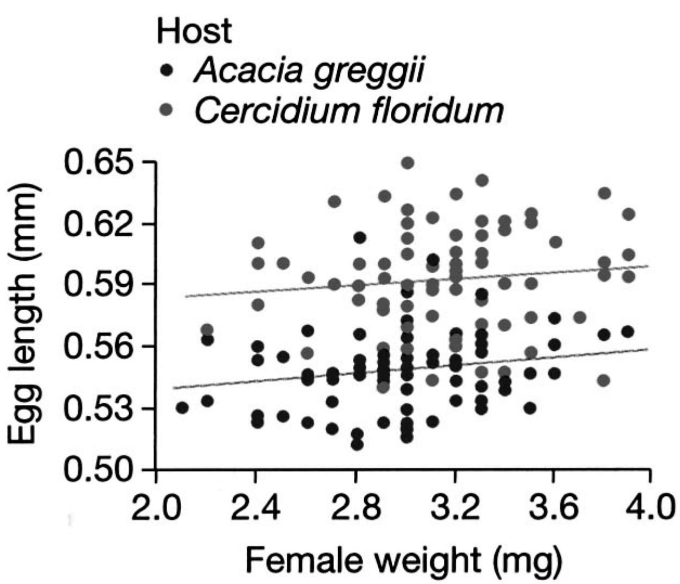
Predicts larger offspring on poorer hosts.

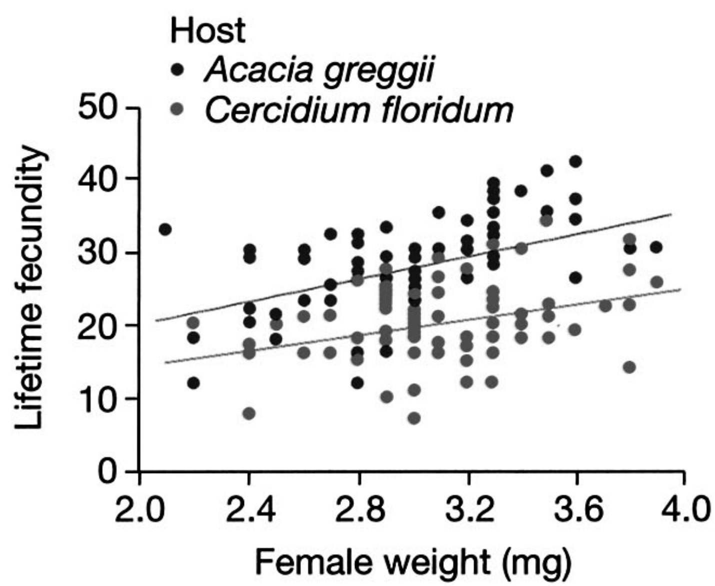


Facultative egg size



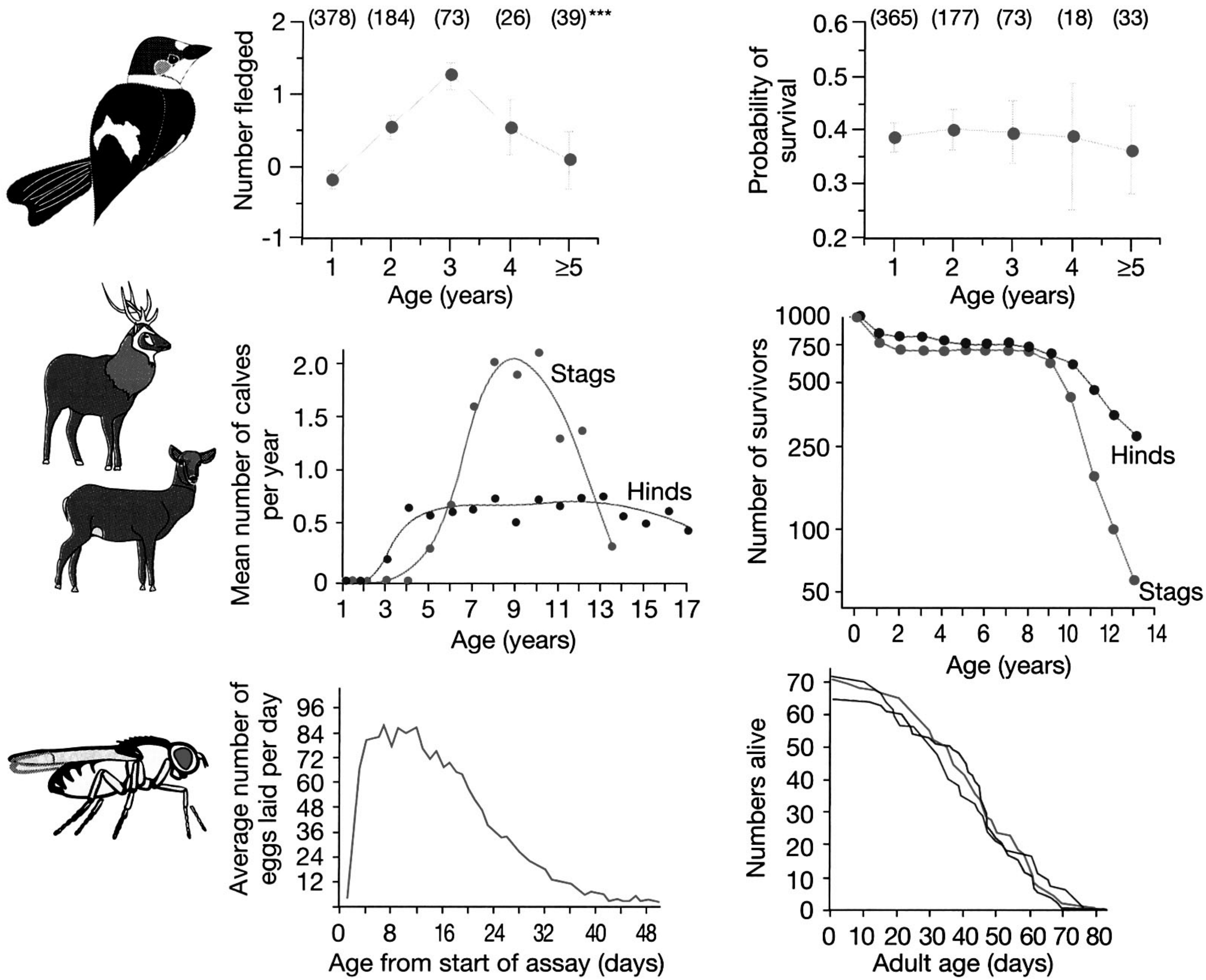






Senescence

- Late life decline in individual fertility and probability of survival
- Aging reduces mx component of fitness (reproduction)
- And reduces lx component of fitness (longevity)
- Aging should be selected against



Number fledged
(378) (184) (73) (26) (39)***
2
1
0
-1
1 2 3 4 ≥5
Age (years)
Probability of survival
(365) (177) (73) (18) (33)
0.6
0.5
0.4
0.3
0.2
1 2 3 4 ≥5
Age (years)
Mean number of calves per year
2.0
1.5
1.0
0.5
0
Stags
Hinds
1 3 5 7 9 11 13 15 17
Age (years)
Number of survivors
1000
750
500
250
100
50
Hinds
Stags
0 2 4 6 8 10 12 14
Age (years)
Average number of eggs laid per day
96
84
72
60
48
36
24
12
0 8 16 24 32 40 48
Age from start of assay (days)
Numbers alive
70
60
50
40
30
20
10
0
0 10 20 30 40 50 60 70 80
Adult age (days)

Theories of aging

- Rate of living
  - Wear and tear
  - Individuals repair as much as possible, but can't keep up
- Evolutionary theory
  - Allocation to repair traded for allocation to reproduction

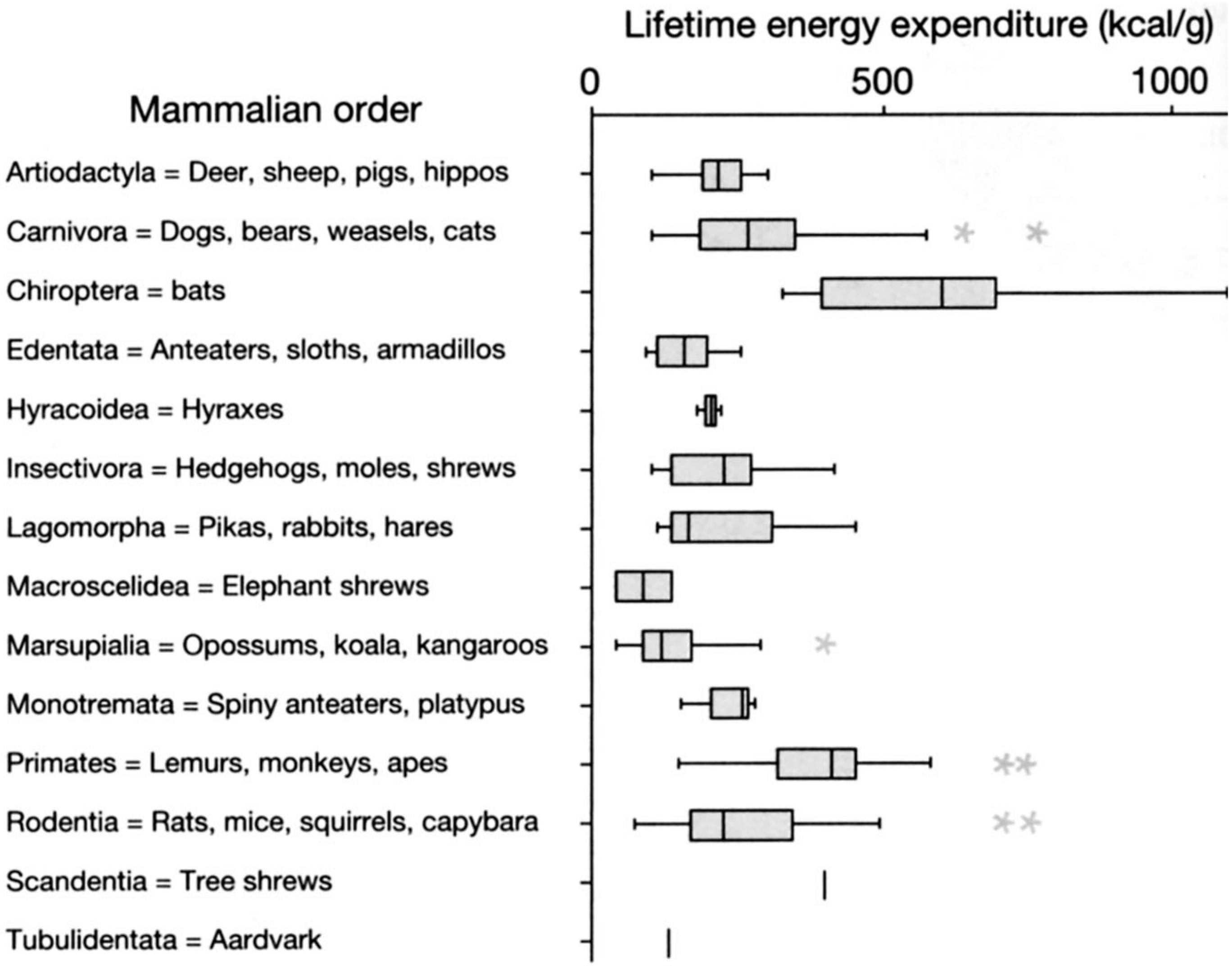
Rate-of-living

- Physiological limit to repair
  - Organisms maximize that repair limit
- Predicts:
  - Aging rate correlated with metabolic rate
  - Organisms should not be able to evolve longer life spans

Aging rate and metabolism

- Predicts all organisms use same amount of energy over their lifetime
- Results: energy/gram/lifetime variable

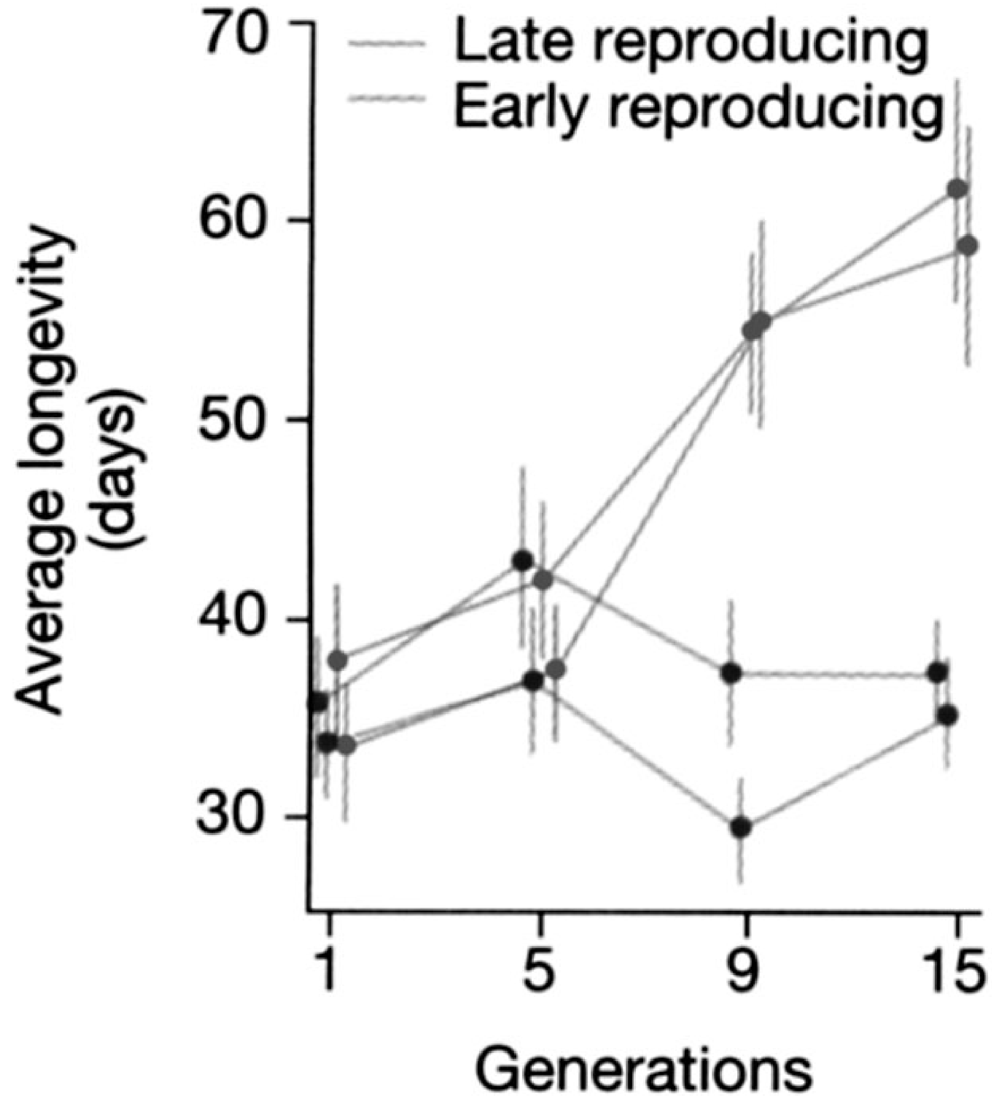
Mammalian lifetime energy use



Can lifespan evolve?

- Select early reproducing individuals
  - Then ones who die young or middle aged still reproduce and pass on genes
- Select late reproducing individuals
  - Then ONLY those individuals who lived that long pass on their genes
  - Genes associated with early death selected out

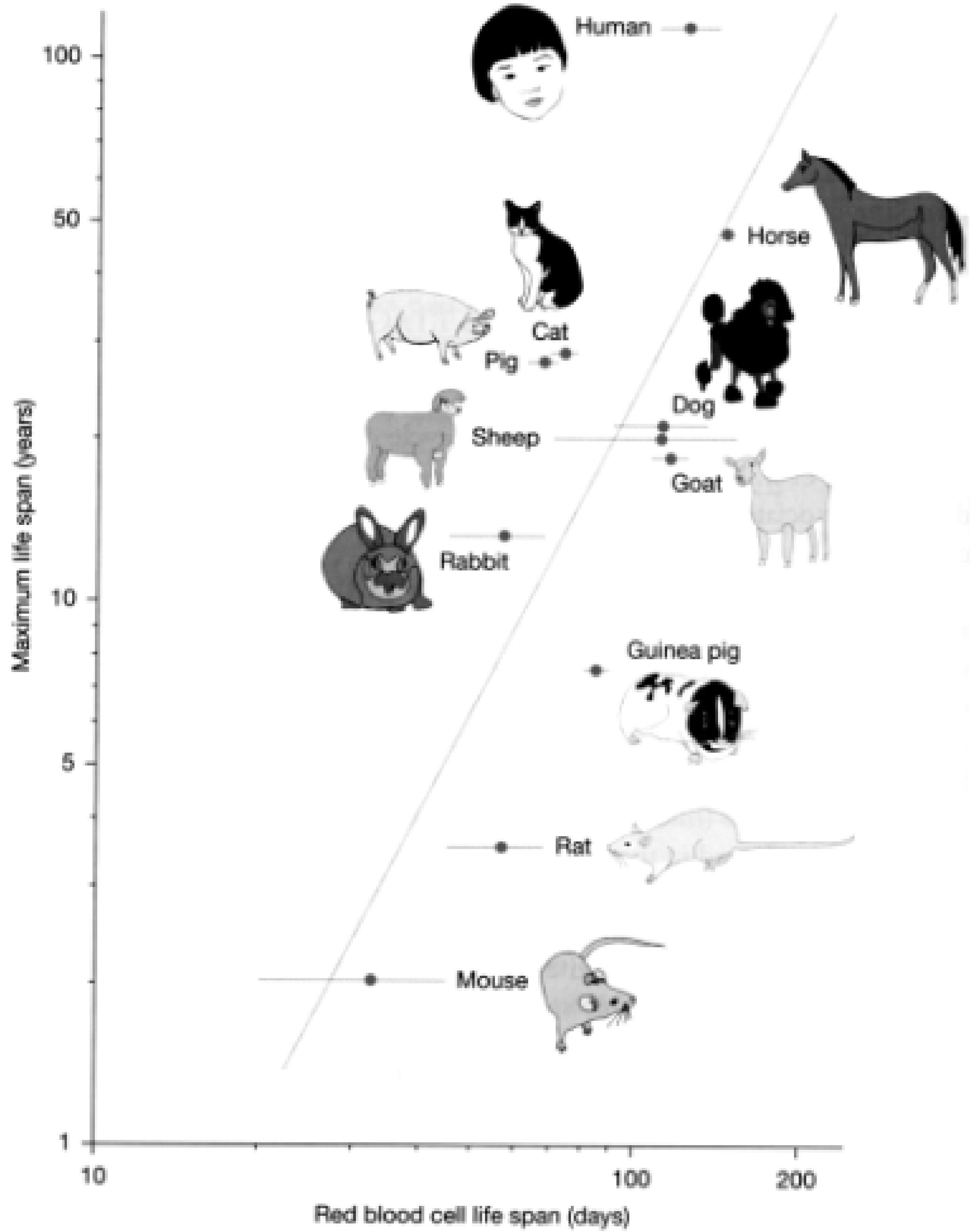
Drosophila results



What about cellular wear and tear

- Two examples
  - Cell death correlated to lifespan
  - Telomeres constrain number of cell divisions

Cells and longevity



Telomere length

- Telomere portion of chromosome arm ‘cap’
- Repeated sequence, humans TTAGGG
- Produced by enzyme telomerase
- Portion lost with DNA replication and cell division
- May limit number of time a cell can divide

Proximate and Ultimate

- Proximate mechanisms:
  - How things operate.
- Ultimate mechanisms:
  - Why things are the way they are.
- Telomere senescence is a mechanism
  - *how* things age
  - But *why* don't organisms simply up regulate telomerase?

The evolutionary explanation: *why* we age

- Organisms fail to repair damage
- Not because they can’t, but because:
  - Deleterious mutations acting late in life
  - Trade-off with reproduction

Late acting deleterious mutations

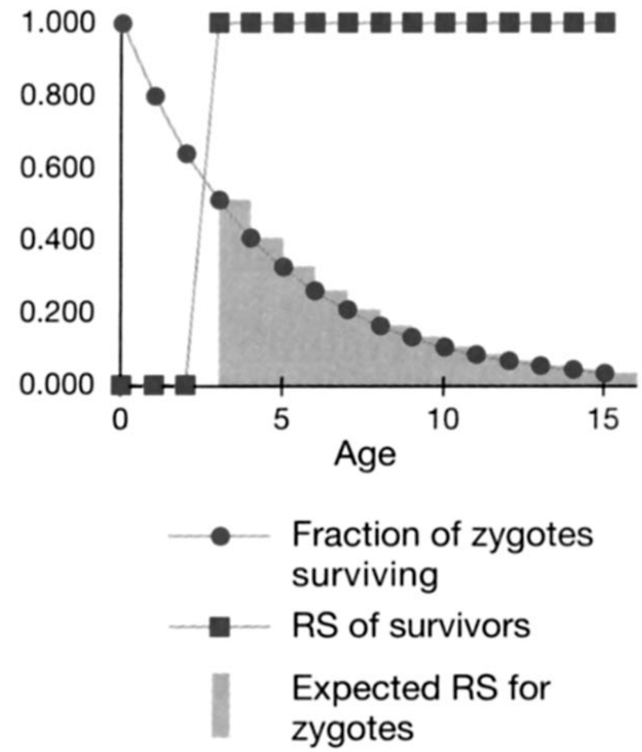
- Senescence is *intrinsic* decline
  - The organism itself has lower reproductive output and higher chance of mortality
- Affected by *extrinsic* risk of mortality
  - External risk of predation, disease, etc.

Wild-type life table

(a) Wild type matures at age 3 and dies at age 16; prior to age 16 annual rate of survival = 0.8

Age	Fraction of Zygotes Surviving	RS of Survivors	Expected RS for Zygotes
0	1.000	0	0.000
1	0.800	0	0.000
2	0.640	0	0.000
3	0.512	1	0.512
4	0.410	1	0.410
5	0.328	1	0.328
6	0.262	1	0.262
7	0.210	1	0.210
8	0.168	1	0.168
9	0.134	1	0.134
10	0.107	1	0.107
11	0.086	1	0.086
12	0.069	1	0.069
13	0.055	1	0.055
14	0.044	1	0.044
15	0.035	1	0.035

Expected lifetime RS: 2.419

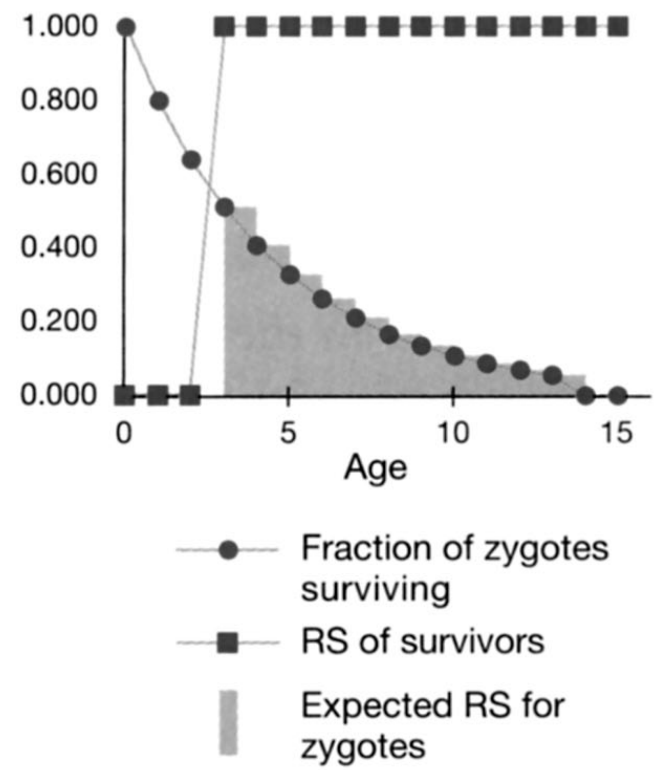


Late acting deleterious life table

(b) Mutation that causes death at age 14; prior to age 14 annual rate of survival = 0.8

Age	Fraction of Zygotes Surviving	RS of Survivors	Expected RS for Zygotes
0	1.000	0	0.000
1	0.800	0	0.000
2	0.640	0	0.000
3	0.512	1	0.512
4	0.410	1	0.410
5	0.328	1	0.328
6	0.262	1	0.262
7	0.210	1	0.210
8	0.168	1	0.168
9	0.134	1	0.134
10	0.107	1	0.107
11	0.086	1	0.086
12	0.069	1	0.069
13	0.055	1	0.055
14	0.000	1	0.000
15	0.000	1	0.000

Expected lifetime RS: 2.340

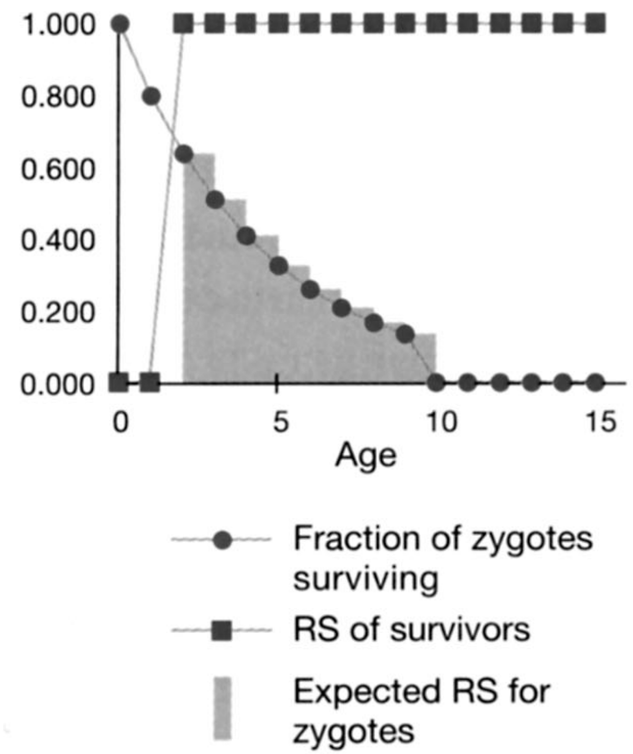


Antagonistic pleiotropy:
early acting beneficial, late acting deleterious

(c) **Mutation that causes maturation at age 2 and death at age 10; prior to age 10 annual rate of survival = 0.8**

Age	Fraction of Zygotes Surviving	RS of Survivors	Expected RS for Zygotes
0	1.000	0	0.000
1	0.800	0	0.000
2	0.640	1	0.640
3	0.512	1	0.512
4	0.410	1	0.410
5	0.328	1	0.328
6	0.262	1	0.262
7	0.210	1	0.210
8	0.168	1	0.168
9	0.134	1	0.134
10	0.000	1	0.000
11	0.000	1	0.000
12	0.000	1	0.000
13	0.000	1	0.000
14	0.000	1	0.000
15	0.000	1	0.000

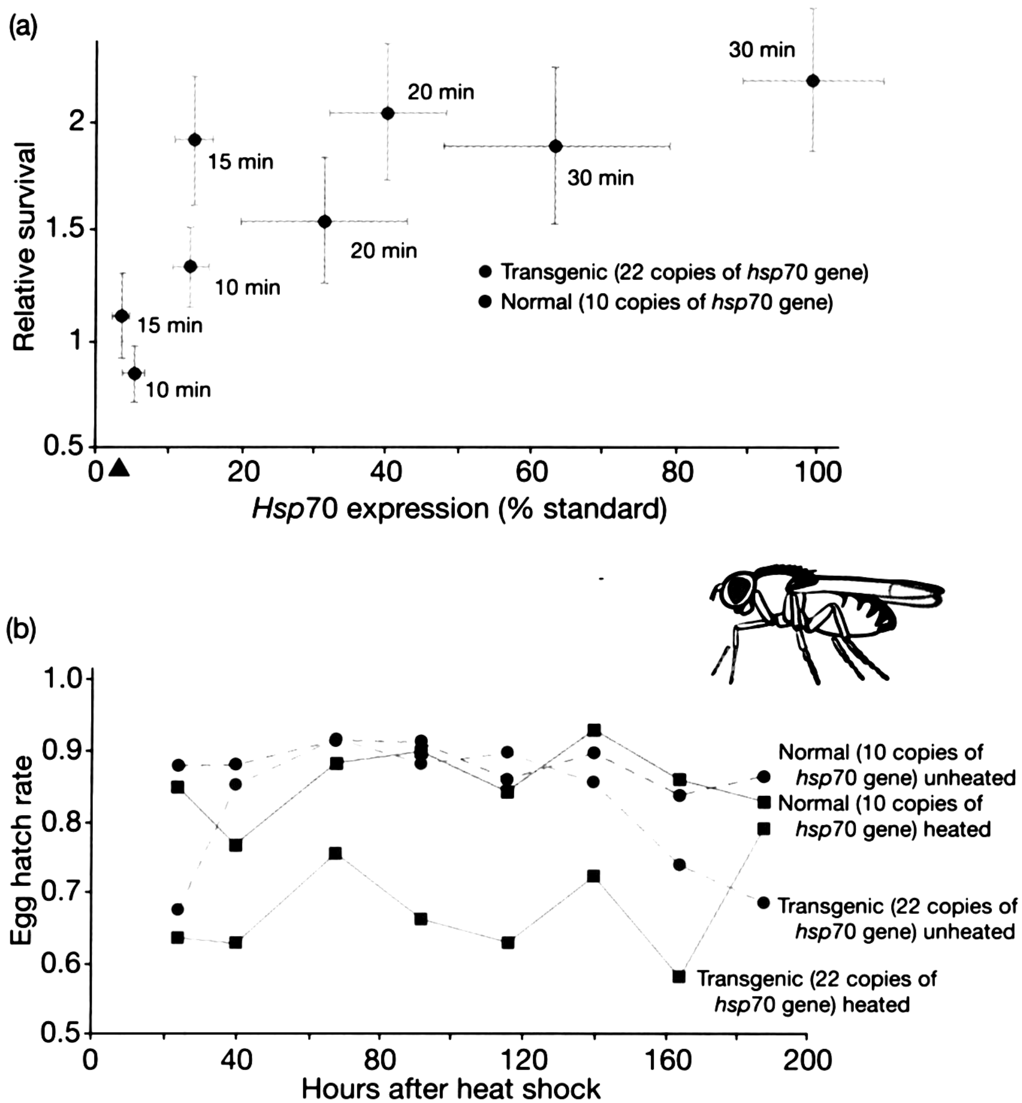
Expected lifetime RS: 2.663



Examples

- Deleterious late acting mutation
  - Maintained by selection-mutation balance
    - Weak selection against
  - Non-polyposis colon cancer, average age 48
- Antagonistic pleiotropy
  - Less repair early, but more reproduction
  - hsp70; hps’s are chaperones

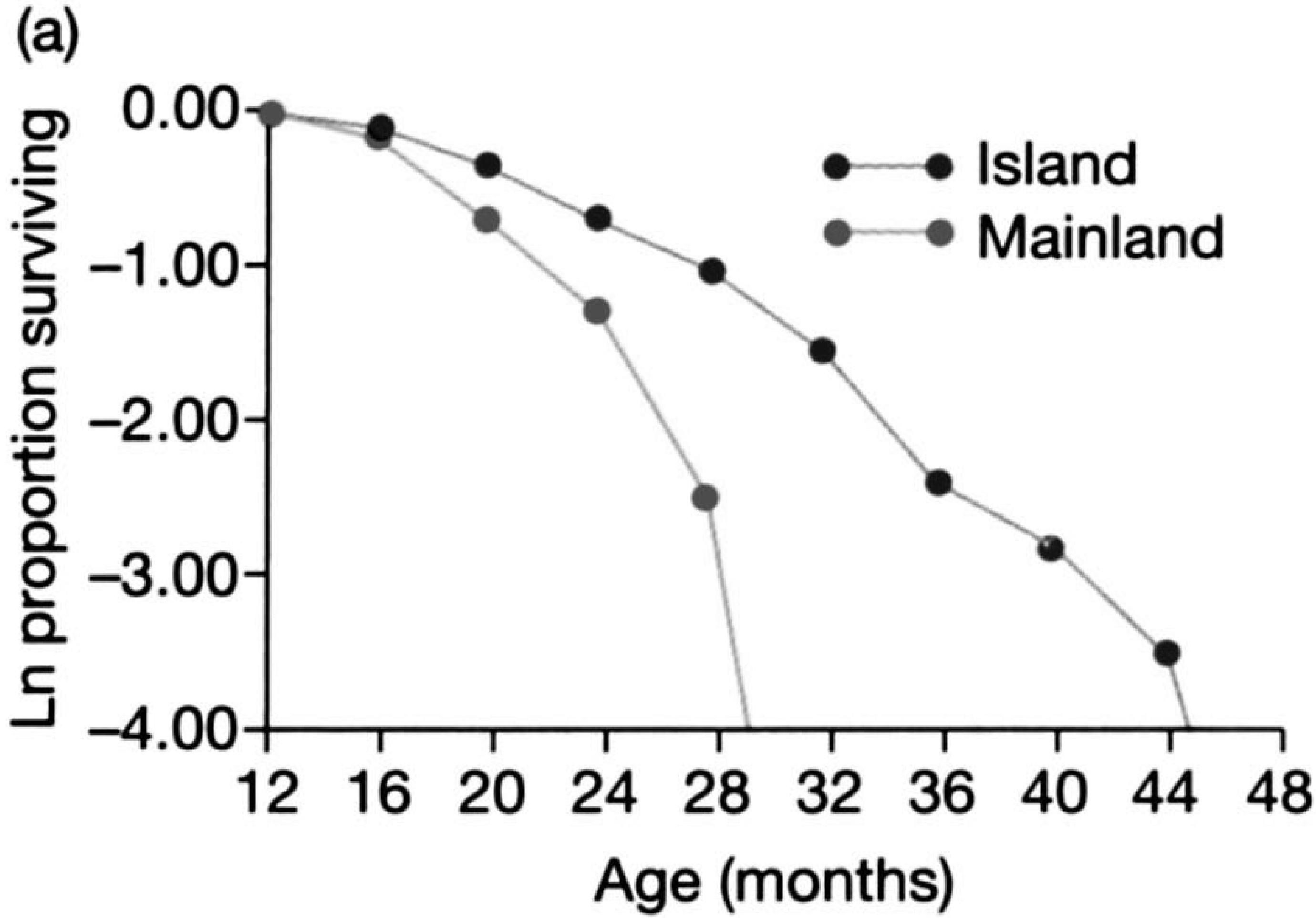
Antagonistic pleiotropy: hsp 70



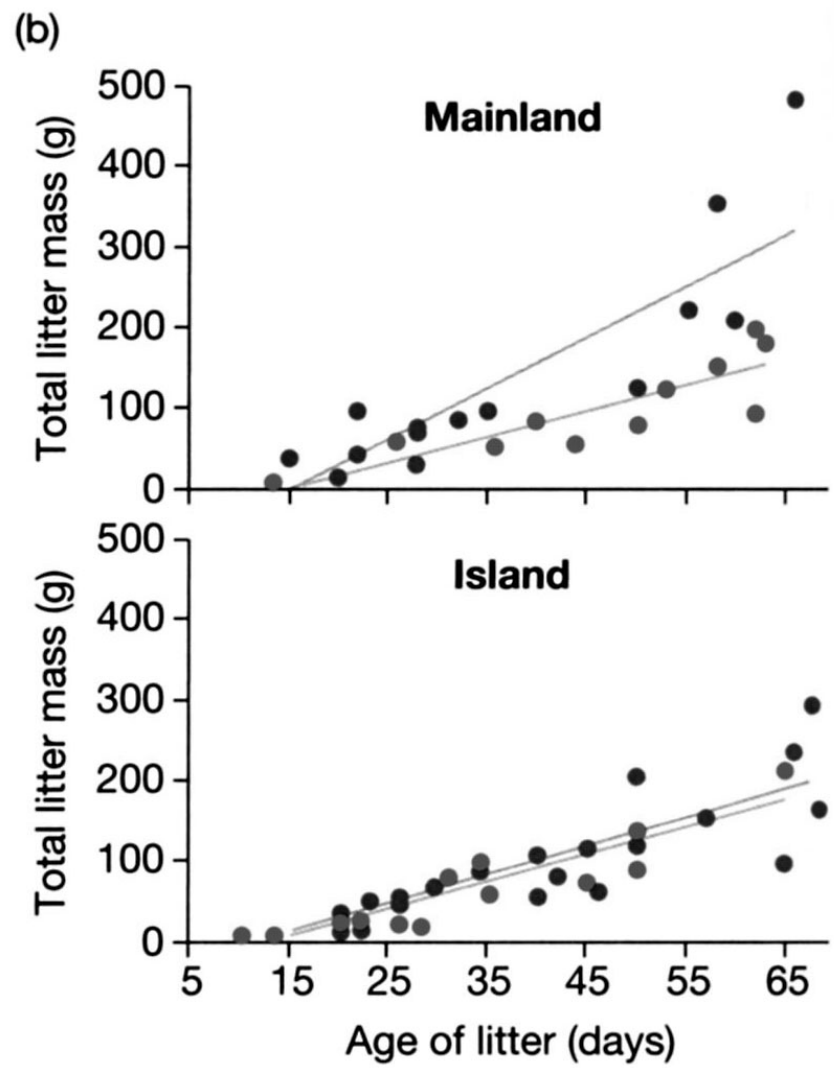
What if chances of dying anyway are high?

- That is, what if *extrinsic* mortality is high?
- Should favor early reproduction
- Should decrease selection for longevity
- Austad studied Virginia opossum
  - Mainland, lots of predators, high extrinsic mortality
  - Island, few predators, low extrinsic mortality

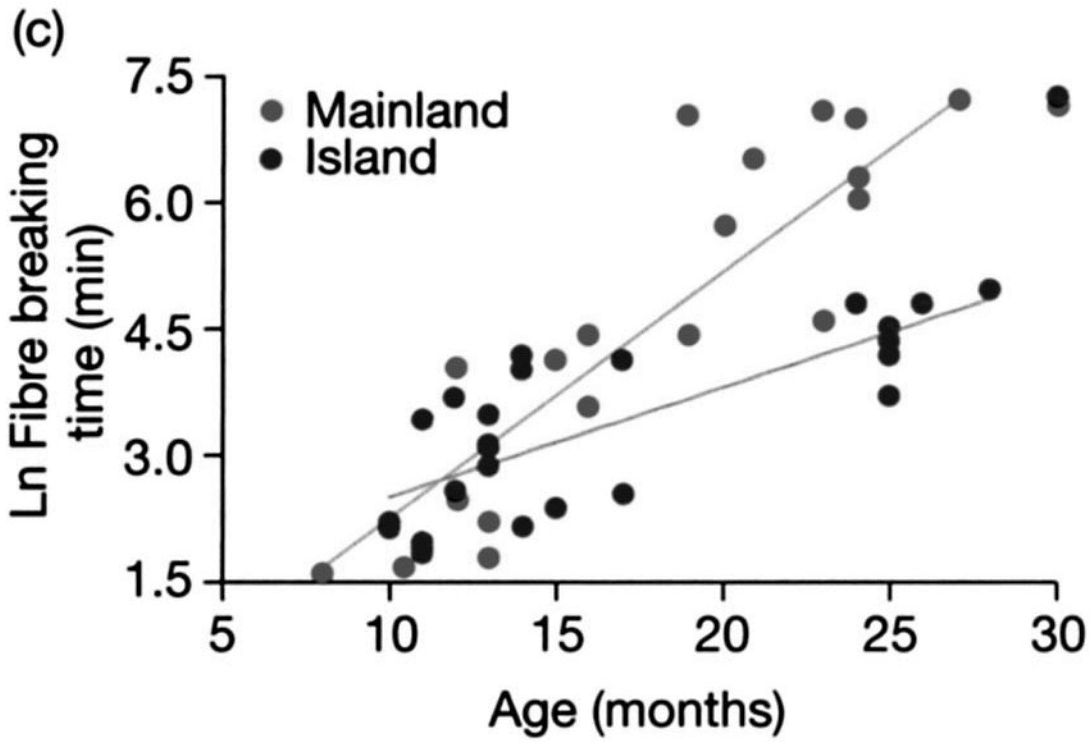
Opossums: island females survive at higher rate



Opossums: island females have year two reproduction (red) same as year one (blue); mainland females show reduced litter provisioning in year two



Opossums: physiological aging



Collagen fibers crosslinked with age; less flexible take longer to break.

Rate of increase (aging) faster on mainland.

Senescence recap:

- Difference b/w *proximate* and *ultimate* explanations
- Senescence occurs *because* selection is weak late in life
  - Extrinsic mortality means few individuals become old anyway
- Genetic mechanisms may be
  - Mutation selection balance (late acting deleterious)
  - Antagonistic pleiotropy
    - Early acting benefit outweighs late acting cost