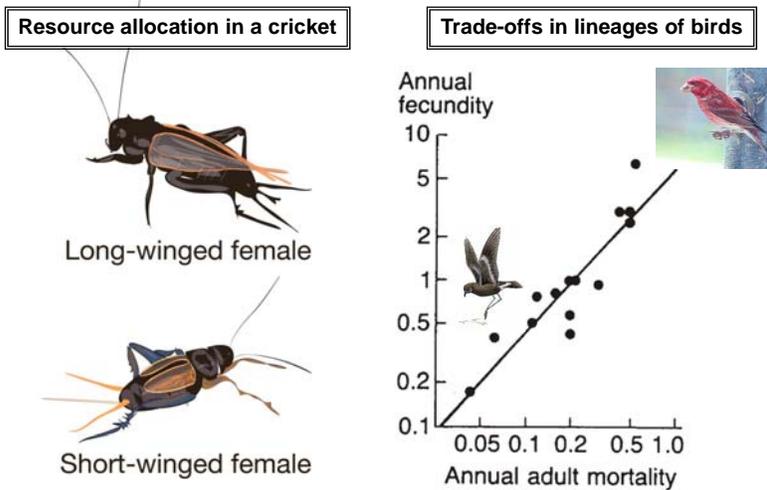


The Evolution of Life Histories



Life histories

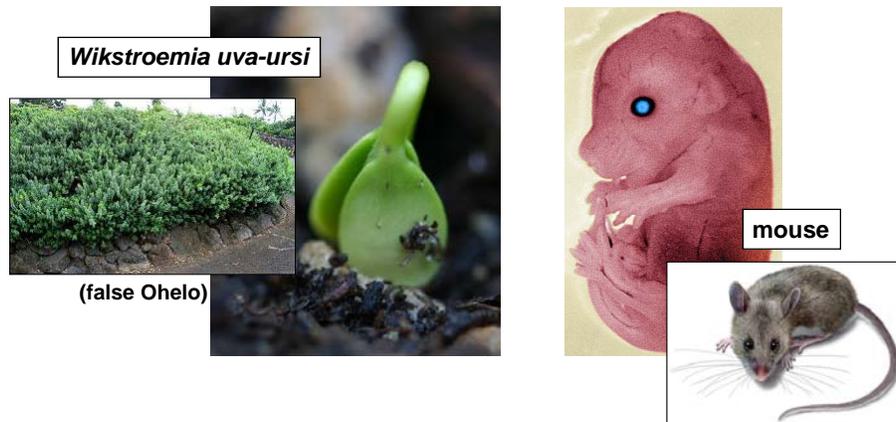
- **The life histories of organisms vary immensely.**
 - Some live to great size and/or great age ([bristlecone](#)), others briefly ([rotifers](#)).
 - Some release millions of propagules each reproductive cycle ([oysters](#)), while others produce 1 huge offspring at a time ([blue whale](#)).
 - Some develop rapidly ([Drosophila](#)), others very slowly ([periodical cicada](#): 17 years a nymph!).
 - Some reproduce once in their life ([century plants](#)), others repeatedly ([perennials](#)).
- There are many ways to achieve high individual fitness. Life history traits **evolve**, responding to selection to achieve the *highest fitness possible under the conflicting circumstances of existence*.



Life history evolution: **size, reproduction, aging, and sex ratio**

- Life history evolution is all about solutions to the fundamental question of life that all organisms must answer:

How should the newly fertilized zygote (assuming sexual reproduction) live the life it is about to begin?



This ultimate question can be broken down into bite-sized pieces:

- At what **age** and **size** should reproduction begin?
- Should offspring be....
 - few** in number but high in quality and **large** in size, or...
 - small** and **numerous**, but less likely to survive on an individual basis?
- How many times** should reproduction occur in a lifetime?
- How much **energy** and **time** per bout should be allocated to...
 - maintenance,
 - growth, and...
 - reproduction?
- Should reproduction be concentrated...
 - early in life** with a short lifespan as a consequence, or should...
 - less energy be put into each bout, accompanied by a **longer life**?
- How many offspring should be **male vs. female**? And should that decision....
 - depend on ecology or social circumstances?
 - be fixed at birth?
 - if sequential, start as male and turn female, or vice versa?

Basic life history traits

Life history traits are components of **fitness**, measured as **reproductive success**.

Life history traits are those that affect the *growth rates of populations*. Basic life history traits include:

1. Individual growth, maintenance, and body size.
2. Ages at which reproduction begins and ends.
3. Number of offspring produced at each age.
4. Potential life span.

For **semelparous** (one-bout) organisms: $R = LM$

R = reproductive success, or the number of descendants of an average female after one generation.

L = probability of an average female's survival to reproductive age.

M = average number of offspring per survivor (fecundity).

Reproductive success in iteroparous species (a simple life table)

x	l_x	m_x	$l_x m_x$
0	1.00	0	0
1	0.75	0	0
2	0.50	4	2
3	0.25	8	2
4	0.10	0	0
5	0.00	0	0
$\Sigma = R$			4

$R = \sum l_x m_x$

x = age

l_x = probability of surviving to age x (i.e. proportion of eggs or newborns that survive to age x)

m_x = average fecundity (# eggs or newborns) at age x

In this case, each female is replaced, on average, by $R = 4$ offspring.

This sum is also the growth rate, per generation, of the genotype.

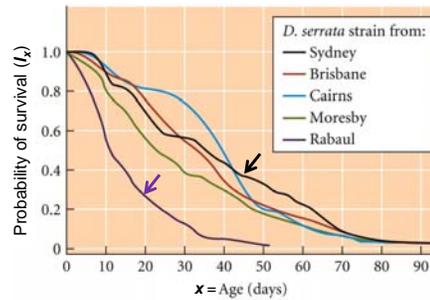
Genetic variation in life-history characteristics in *Drosophila serrata* from 5 localities in Australia:



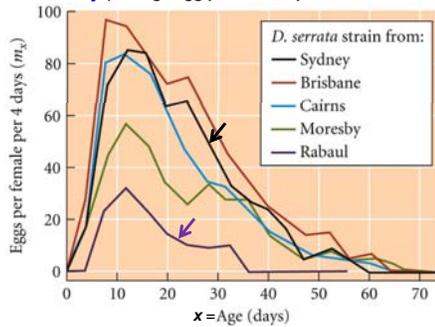
Here, l_x (survival rate) and m_x (fecundity) are shown for different populations.

These data also imply that life history traits are heritable.

Survivorship (fraction of newborns that survive to each age)



Fecundity (average egg production per female at each age)



R vs. r

- **R** is a measure of *reproductive success per generation*.
- But different genotypes might differ in the length of a generation.
- So rather than using **R**, it is better to use **r**, which is the *per capita rate of population increase per unit time* (not per generation).
- But the general analysis just presented gets across the idea, because just like **R**, **r** depends on the *probability of survival and fecundity at each age*.

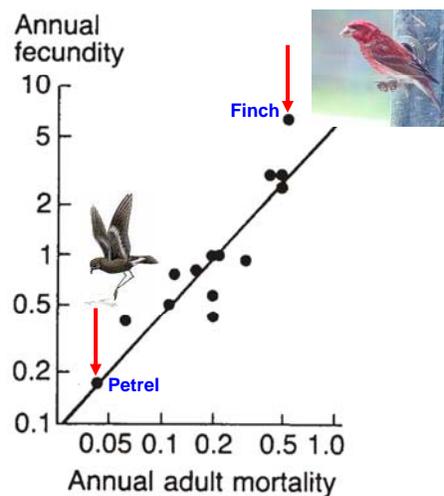
(not to be confused with **r**, the coefficient of relatedness...)

Life history evolution: **The concept of the trade-off**

- **Expectation:** organisms should evolve ever greater fecundity, ever longer life, ever larger body size, and ever earlier maturity.
- But the ideal organism does not exist. Evolution is the end result of *many conflicting forces*.
- *Example:*
 - Being large is good – you can have more offspring, both in mass and numbers.
 - But it takes time to grow large: You may die before ever reproducing at all!
- Trade-offs are inherent when you must *divide up finite resources* – a process known as the *allocation of resources* – among...
 - maintenance
 - current reproduction
 - growth and storage (bet-hedging for future reproduction)

Trade-offs in lineages of birds

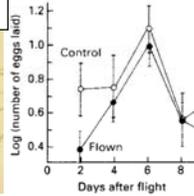
(a phylogenetic pattern)



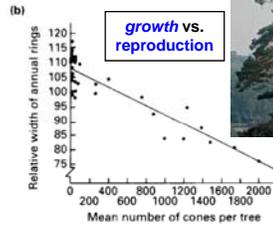
A potpourri of life history trade-offs

Induced flight in *Drosophila subobscura*
(Inglesfield & Begon 1983)

activity vs. reproduction



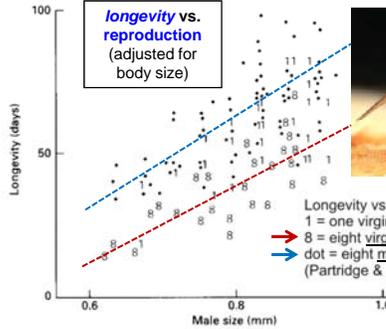
growth vs. reproduction



The **life history strategy** of an organism can be thought of as a *suite of adaptations that resolves conflicts over allocation of limited time and other resources.*

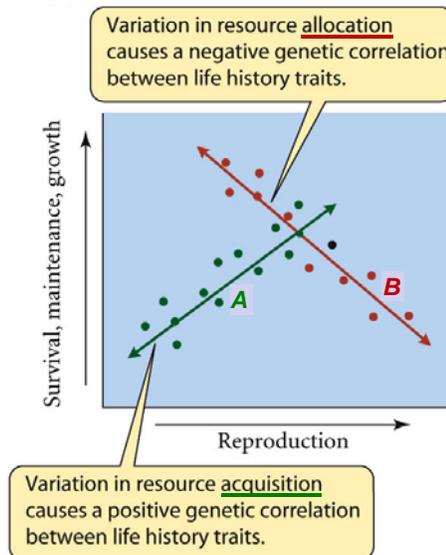
(c)

longevity vs. reproduction (adjusted for body size)



Life history traits are **connected by trade-offs**

- Resources are first acquired, then allocated, e.g. acquired energy is divided between maintenance/growth and reproduction.
 - Variation at **locus A** affects the amount of a resource that an individual acquires from the environment.
 - Variation at **locus B** affects the allocation of that resource to different functions.
-
- Trade-offs often show genetic correlations, because some of the same genes will affect both traits – pleiotropy.
 - e.g., genes for *size* & *fecundity* show positive correlations, perhaps because they're the same gene!



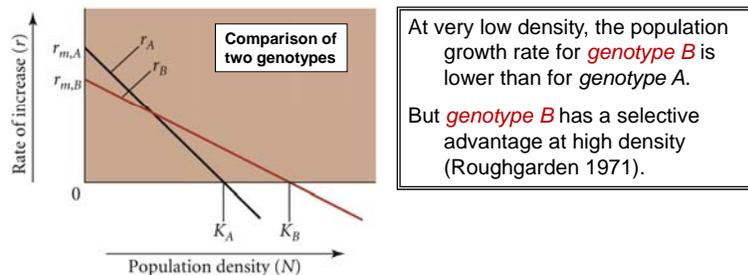
Optimality in life-history theory: a caveat

- Wherever there are trade-offs, a **cost-benefit analysis** is appropriate.
- **Expectation:** Organisms will evolve to the point where the **net benefit is maximized** – thereby attaining the *optimal compromise*.
- Normally, such an analysis is straight-forward.
- But cost-benefit, and optimality, assume that when an optimal solution is found, it is **optimal for the whole population**.
 - **Not** necessarily true – note the useful example of **sex ratio**:
 - If an organism can control the sex ratio of its offspring, then the best ratio depends on the sex ratios produced by other organisms in the population. Why? **Because the rarer sex will be at an advantage.** (More on sex ratio later.)
 - This is **frequency dependence** – in this case, *negative* frequency dependence.

The concept of optimality, continued.

- So in life history evolution, one has to distinguish between optimality and frequency dependence.
 - **Optimality** = a world at equilibrium.
 - **Frequency dependence** = a changing world; your best strategy depends on what others do.

Example, showing density-dependent selection on rates of increase:



A. J. Lotka



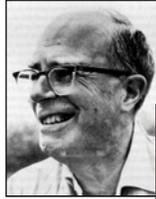
A short history of life history studies

- Darwin considered life histories, but not a lot.
- Weismann argued for **adaptive aging** caused by natural (but group) selection – late 1800s.
- A. J. Lotka and R. A. Fisher pioneered **life table analyses** – in the 1930s.
- Ten years later: R. Moreau & David Lack on **clutch size** in birds (Lack's work stressed an experimental rather than quantitative approach).
- G. C. Williams weighed in (1957 – he was 30) on the evolution of **senescence**.
- A. W. F. Edwards, W. A. Kolman, H. Kalmus & C. A. B. Smith developed treatments of the 1:1 **sex ratio** (1960; several papers).
- M. L. Cody (1966) applied Richard Levins' idea of fitness sets to life history evolution, and first spoke of **adaptation as the resolution of conflict in allocation** of time and energy.

R. A. Fisher



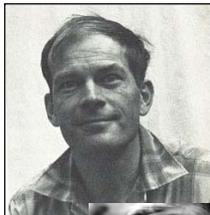
D. L. Lack



M. L. Cody



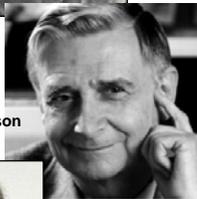
R. H. MacArthur



A short history, continued (mostly 1966)

- Also in 1966, Cody introduced the idea that different life history adaptations are favored under high vs. low **population density** (relative to the carrying capacity – **K** -- of the environment).
- These suites were named **r-selection** and **K-selection** by Robert MacArthur & E. O. Wilson in *The Theory of Island Biogeography* (1967).
- G. C. Williams (1966) quantified *present* and *future* components of fitness in the uniform currency of ***reproductive value**, based on life table calculations.
- Also in 1966, W. D. Hamilton specified the basic **scaling forces** for natural selection (on **fecundity & survival**) over the entire life history – see Rose et al. 2007 for a retrospective.
- Reviews in D. Roff (1992), Stephen Stearns (1992), and Brian Charlesworth (1994).

E. O. Wilson



Derek Roff



S. Stearns

* The expected reproduction individuals **from their current age onward**, given that they have survived to their current age. (R. A. Fisher 1930)

Understanding life history traits

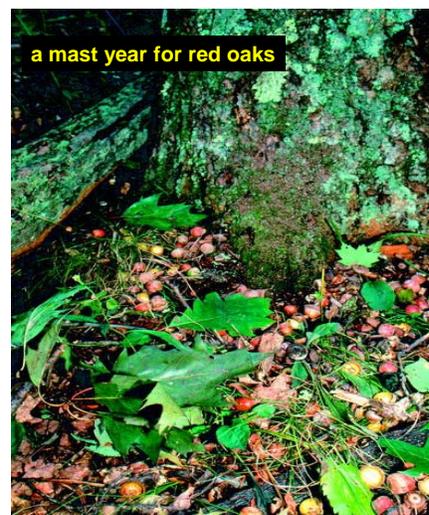
Three fields contribute to explaining the evolution of life histories:

- I. **Demographics:** Life history traits depend on *population structure* – the *age, size, and reproductive output* of its constituent members.
 - For example, selection on reproductive performance is stronger on younger than older adults, because they contribute more to the instantaneous growth rate of the population.
 - An increase in mortality at any stage of life *devalues* older individuals, because those are now less likely to reproduce.
- II. **Genetics:** Life history traits are polygenic – i.e., quantitative traits.
 - This means understanding them with quantitative genetic techniques.
 - For life history traits to evolve, they must show *heritability*.
 - Depending on h^2 , a portion of life history variation may be environmental – i.e., phenotypically plastic. This may be a good thing, so an individual can *switch strategies* during its lifespan.
- III. **Phylogenetics:** Life histories have evolved in a phylogenetic context.
 - As such, *comparative methods* are appropriate and informative.
 - One can tease out *constraints* or *fixed effects* due to inheritance of a trait from a common ancestor.

Understanding life history traits I: Demography

Under this heading, we can address a few of those fundamental questions of life.

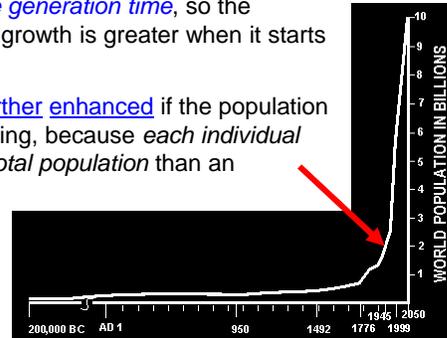
1. At what **age** should I start to reproduce?
2. At what **size** should I start to reproduce?
3. How **many offspring** should I produce at a time?
4. How **often** should I reproduce during my lifetime?
5. How **long** should I live?



Demography: *Age at first reproduction*

Because aging – senescence – begins at maturation, the **earlier** you start reproducing, the better.

- Life is **risky**. Earlier reproduction means you're more likely to breed before you die because of some environmental hazard, e.g. predation, disease, or accident.
- Earlier reproduction also **shortens the generation time**, so the individual's **contribution** to population growth is greater when it starts breeding at a younger age.
- Advantage of early reproduction is **further enhanced** if the population size is **increasing** rather than decreasing, because *each individual born today is a larger fraction of the total population* than an individual born in the future.



Note the difference in I_x between ages 2 and 3

x	I_x	m_x	$I_x m_x$
0	1.00	0	0
1	0.75	0	0
2	0.50	4	2
3	0.25	8	2
4	0.10	0	0
5	0.00	0	0
$\Sigma = R$			4

same $R!$
(contribution to population growth)

$R = \Sigma I_x m_x$

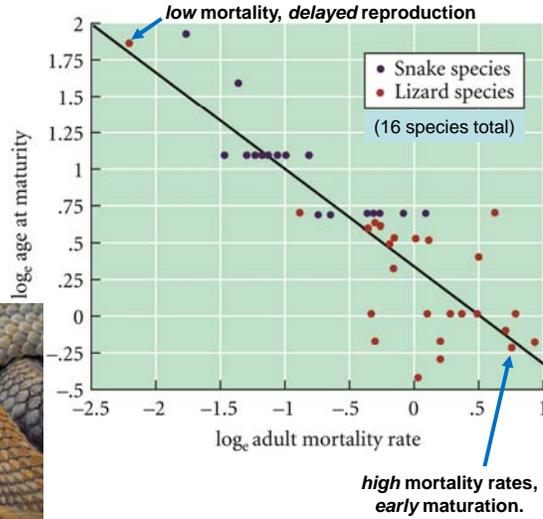
x = age
 I_x = probability of surviving to age x (i.e. proportion of eggs or newborns that survive to age x)
 m_x = average fecundity (# eggs or newborns) at age x

Age at first reproduction is also (inversely) correlated with mortality rate.

Age at first reproduction vs. adult mortality rate:

Snakes & lizards (Shine & Charnov 1992)

- The **lower** the annual mortality rate of adults, the **later** reproduction is selected to begin.
- Delayed onset of reproduction is most likely to evolve in species with high rates of adult survival.



Individual fecundity (# eggs) in a hypothetical population as a function of **life span** and **age at first reproduction (a)**

		Life span								
		1	2	3	4	<u>5</u>	6	7	8	
Age at first reproduction	1	10	20	30	40	50	60	70	80	360
	2	0	20	40	60	80	100	120	140	560
	3	0	0	30	60	<u>90</u>	120	150	180	630
	4	0	0	0	40	80	120	160	200	600
	5	0	0	0	0	50	100	150	200	500
	6	0	0	0	0	0	60	120	180	360

Note that with each year's delay in reproduction, fecundity goes up by **10** offspring as body size increases. (assuming **semelparity**; follow arrows)

Blue typeface = most productive age-at-first-reproduction for a given life span.

Demography: *Size at first reproduction*

Generally, the bigger you are when you first reproduce, the better.

1. You can produce a **larger number of offspring**.
 - Larger mass means more offspring at a time – larger organisms are more fecund.
2. You can provide **better parental care**. Larger size means...
 - more nutrients to the unborn, as yolk or larger propagule size,
 - easier acquisition of more resources for your young,
 - and better protection for your young.
3. You can be better at **intra- and intersexual competition**. Larger size means...
 - winning contests with other males,
 - and attracting females by virtue of your 'handicap'.

Small organisms are **not** small because it improves fecundity or lowers mortality. **They are small because *it takes time to grow large***, and with heavy mortality, the investment in growth would never be paid back in increased fecundity.

Size at first reproduction

Example from the **sea lion** *Zalophus californianus*, which has a harem-style mating system

Males weigh in at 600 lbs. and mature at age 11 or 12.



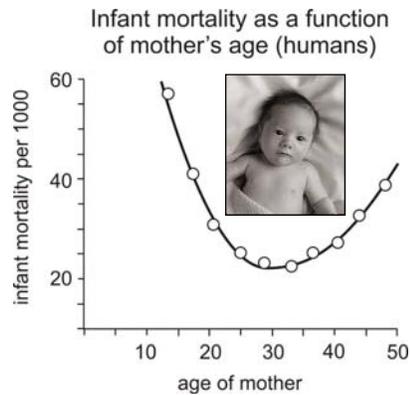
If a male tries to secure a harem at a smaller size, he will fail, and likely be killed as well.

Females are much smaller than males (200 lbs), and become sexually mature at 5 or 6 years of age.

Size vs. age in conflict

- **Sea lion**: size and age (at first reproduction) are in conflict.
- larger size requires time → later start to reproduction.
- *So despite the advantages of early reproduction, there are benefits to delayed maturation.*

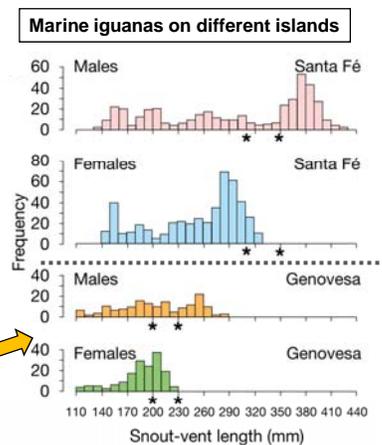
Parental care vs. age of mother



This does *NOT* mean that the optimal age of reproduction is 30. Rather, it is somewhere *between 15 & 30* – a compromise between *early reproduction* and the *experience of age*.

Selection can change life-history optima:

- For **body size** evolution, there are optimal solutions to mandatory trade-offs.
- **Marine iguanas** (like the sea lions):
 1. Assume that something, like too little food, is selecting against larger male sea lions.
 2. That *will favor breeding by the smaller males*.
 3. And that could eventually produce *earlier maturation* of individuals in that population.



4. In other words, the favored life-history strategy will depend upon *what others in the population are doing*. Strategies will change.

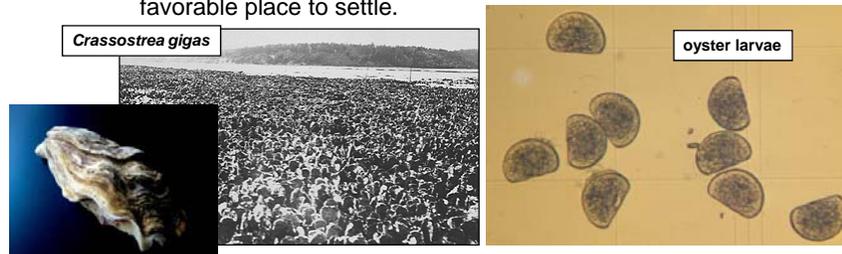
Understanding life history traits I: **Demography**

1. At what **age** should I start to reproduce (earlier or later)?
2. At what **size** should I start to reproduce (small size or large size)?
- 3. How **many offspring** should I produce at a time? (includes propagule **number** and propagule **size**)
4. How **often** should I reproduce during my lifetime (once or many)?
5. How **long** should I live?

Demography: **Fecundity**

Even though “more is better,” there are also life-history “decisions” to be made about the **number** vs. **size** of offspring.

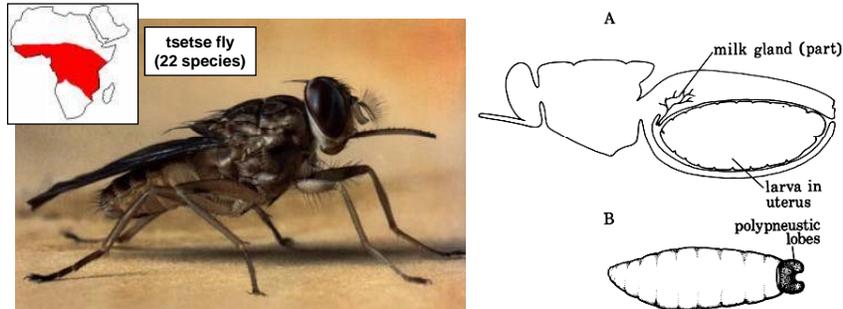
1. **Numerous, tiny offspring** might be produced under conditions of extremely high, unavoidable risk very early in life (**r-selection**).
 - Many plants produce tiny propagules, the vast majority of which will never live to reproduce. The parent ‘floods’ the environment in order to produce a few successful offspring.
 - most mortality results from “non-selective deaths” (accidents)
 - Another **example**: Oysters (and many other bivalve species) produce millions of eggs/zygotes, of which only a few will find a favorable place to settle.



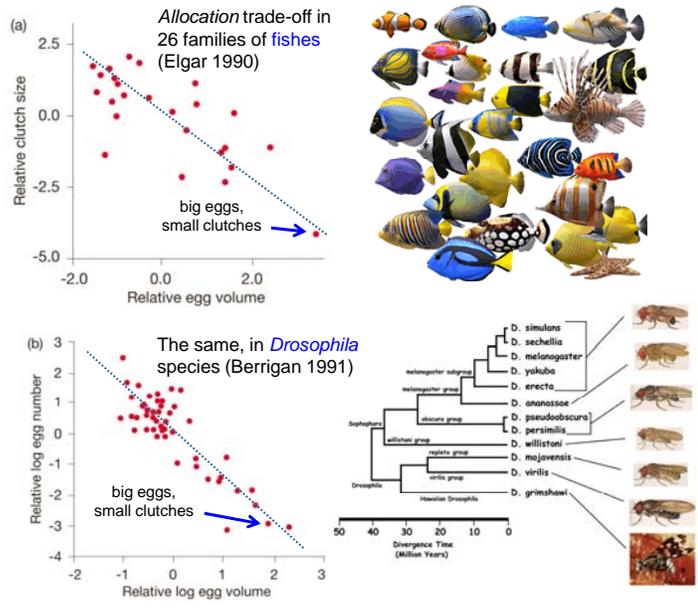
Fecundity

2. **Few, but large, offspring** are favored by selection under more stable, predictable environmental conditions (**K-selection**).

- **Parental care:** mother (or father) invests resources such as food and protection in larger, better developed, but fewer young.
- Even insects: the **tsetse fly** of Africa (*Glossina* spp.), which is a live bearer of one offspring at a time.

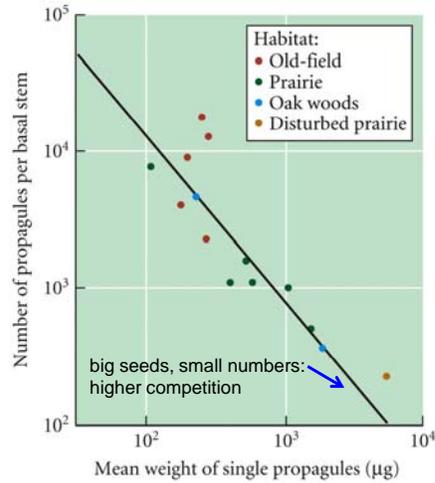


Numbers vs. Quality: you can't have both at the same time



Trade-off of **propagule number** vs. **propagule size** in *Solidago* species, attributable to ecological selection.

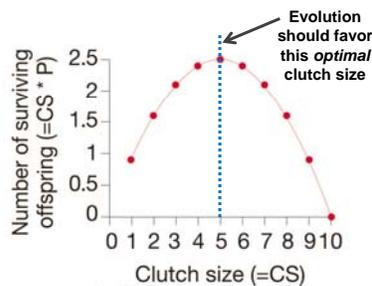
- Colonizing species, growing in old-field habitats, tend to produce **smaller** seeds than species that grow in more stable prairies.
- In the stable habitats, competition is more intense, favoring **larger** seeds (Werner & Platt 1976).
- Suggests that parents must allocate limited resources.



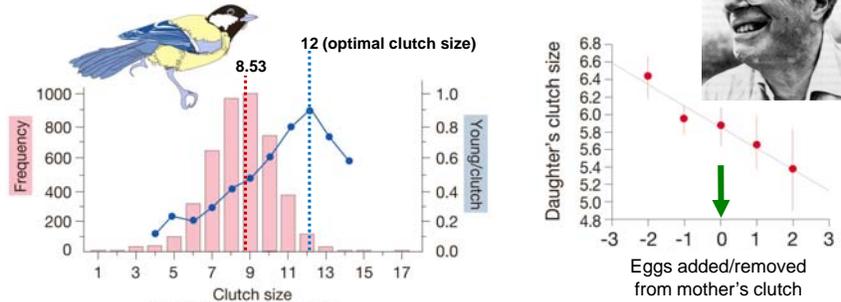
Determining **optimum propagule number**, assuming selection favors the clutch size that produces the most surviving offspring (Lack 1947)

1. Assume a fundamental trade-off: the probability that any offspring will survive decreases with increasing clutch size (Schluter & Gustafsson).
2. The number of surviving offspring is [clutch size] x [probability of survival], which is then graphed against clutch size (propagule number) as **fitness**.

Boyce & Perrins tested this hypothesis in *Parus major* (1987)

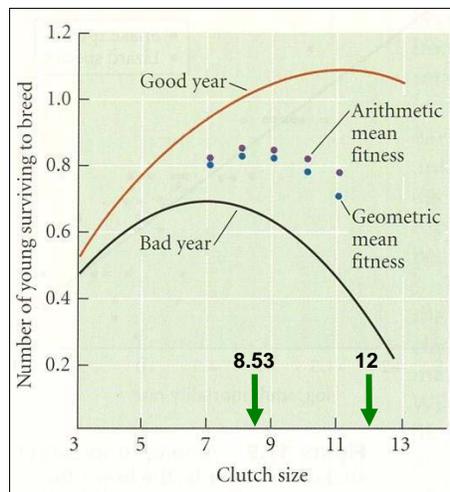


Testing Lack's hypothesis in *Parus major* in Wytham Wood



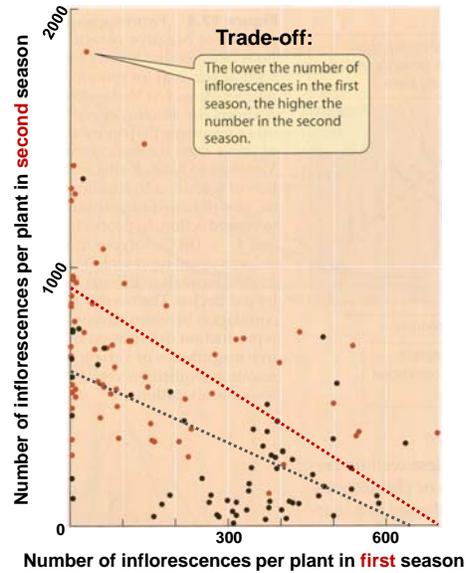
- Data collected from 4,489 clutches monitored from 1960 to 1982 were **inconsistent** with Lack's hypothesis.
 - average clutch size = **8.53**...
 - but the **best offspring survival** occurred in clutches of **12** eggs
- **Explanation**: an additional **trade-off** is operating, between a mother's clutch size in the **first year** and her clutch size in **future years** [not shown].
- In addition, females reared in nests with smaller clutches had higher reproductive success (Schluter & Gustafsson 1993).

Also, note **extensive year-to-year variation** (Boyce & Perrins 1987)



Another example: **number of inflorescences** in two consecutive years

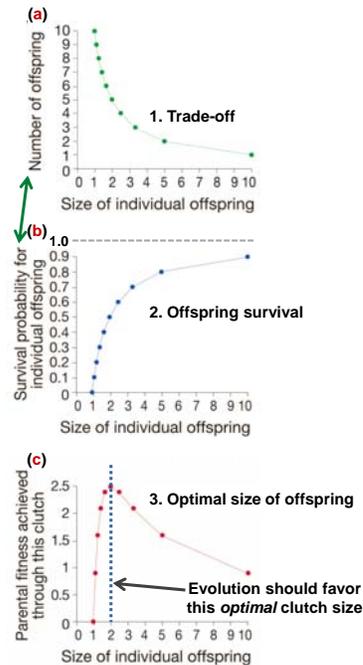
- The turf-grass, *Poa annua*
- The two colors of symbols represent plants from two different habitats, grown together.
- The results demonstrate the *trade-off*, plus a *genetic basis* for cost of reproduction – the two populations differ (Law 1979).



Determining the **optimum propagule size**, based on the number/size trade-off vs. survival.

1. Assume a trade-off between size and number of offspring (**a**).
2. Assume also that individual offspring will survive better if they are larger (**b**).
3. [Of course the survival probability cannot exceed unity (**b**)]
4. Expected **fitness (c)** is [number of offspring] x [probability of survival].
5. Graph the expected fitness against propagule size (**c**).
6. In this case, *increasingly large offspring get progressively smaller survival benefit*, so intermediate size gives the highest parental fitness.

(Theory by Smith & Fretwell 1974)



Demography: *Number of cycles of reproduction*

- An organism can reproduce once, or many times in its lifetime.
 - Once = *semelparity* (includes “annual” and “big-bang” life cycles).
 - Multiple bouts = *iteroparity* (includes “perennial” life cycles)
- **Expectation:** many bouts of reproduction (iteroparity) is better.
But selection pulls organisms in many directions.

- In general, an organism will be selected to engage in additional bouts of reproduction *only if it is likely to survive the first bout.*
- If so, it will be selected to invest *less* in the first bout *in anticipation of future reproduction* – the iteroparous (bet-hedging) strategy.
- So the number of cycles of reproduction is a consequence of simultaneous interactions (including trade-offs) among such factors as:
 - (i) harshness of the environment
 - (ii) mating opportunity
 - (iii) life span.

