Life Is Not A Bed of Roses

Trade-offs in Life History Evolution

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LS2201

Life histories

Organisms differ dramatically in how they develop, the time they take to grow, when they become mature, how many offspring of a particular size they produce, and how long they live. Together, the age-, size-, or stage-specific patterns of development, growth, maturation, reproduction, survival, and lifespan define an organism's life cycle, its life history.

Life history Theory

The principal aim of life history theory, a branch of evolutionary ecology, is to explain the remarkable diversity in life histories among species.

Adaptation by natural selection is based on variation in Darwinian fitness among individuals, and since life history traits determine survival and reproduction they are the major components of fitness.

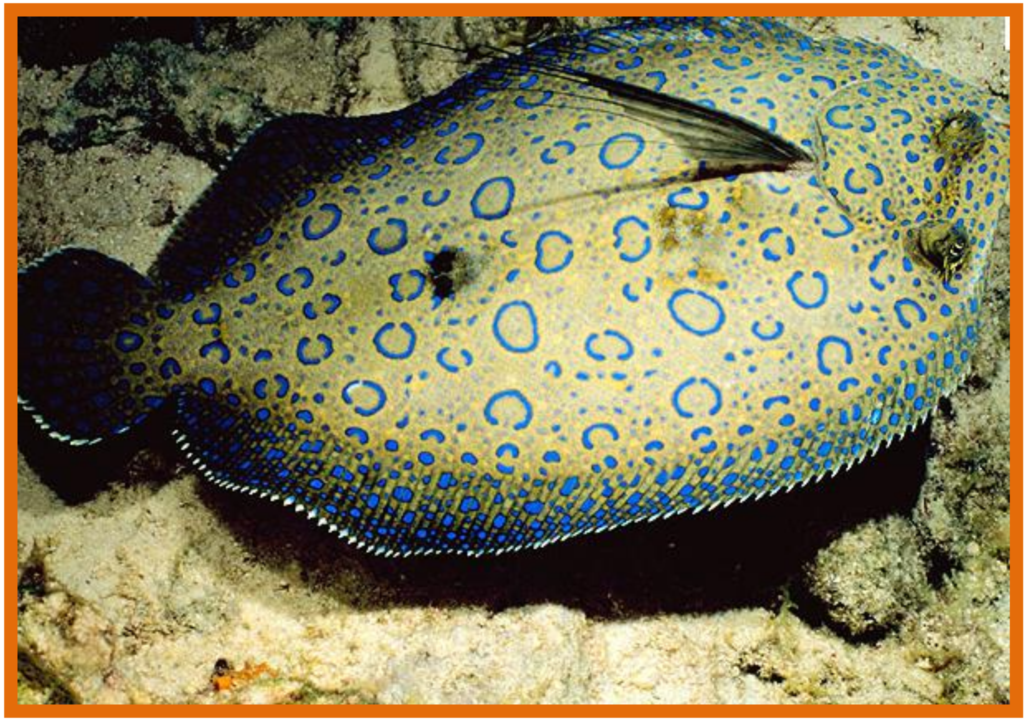
The study of life history evolution is thus about **understanding adaptation**, the most fundamental issue in evolutionary biology.

Life history Theory

Life history theory predicts how natural selection should shape the way **organisms parcel their resources into making babies** (Reznick 2010).

The theory does so by analyzing the evolution of fitness components, so-called **life history traits**, and how they interact: size at birth; growth pattern; age and size at maturity; number, size, and sex of offspring; age-, stage- or size-specific reproductive effort; age-, stage- or size-specific rates of survival; and lifespan.

A diverse array of life histories



Flatfish show huge diversity.

Some tropical species are 2 cm long and reproduce within their first year of life.

The Pacific halibut exceeds 200 cm and takes over 10 years to mature.

Hippoglossoides platessoides off the coast of Scotland mature at 3 years at a length of about 20 cm. The same species takes 15 years to mature at a length of 40 cm in Newfoundland.

The Scottish fish reach a length of 25 cm and live for 6 years, while the Newfoundland fish live for 20+ years at attain a length of 60 cm.

Food

Predators

Shelter

Competitors

Mates

Life history traits

- Age and size at maturity
- Number and size of offspring
- Life span and reproductive investment

Life history evolution: Trade-offs

The amount of energy available is finite.

Energy devoted to one function – such as growth or tissue repair – cannot be devoted to other functions – such as reproduction.

Biological processes are time consuming. If an animal keeps growing without attaining reproductive maturity, it risks dying without reproducing.

Fundamental trade-offs involving energy and time mean that every organism's life history is an evolutionary compromise.

How many offspring should I produce?

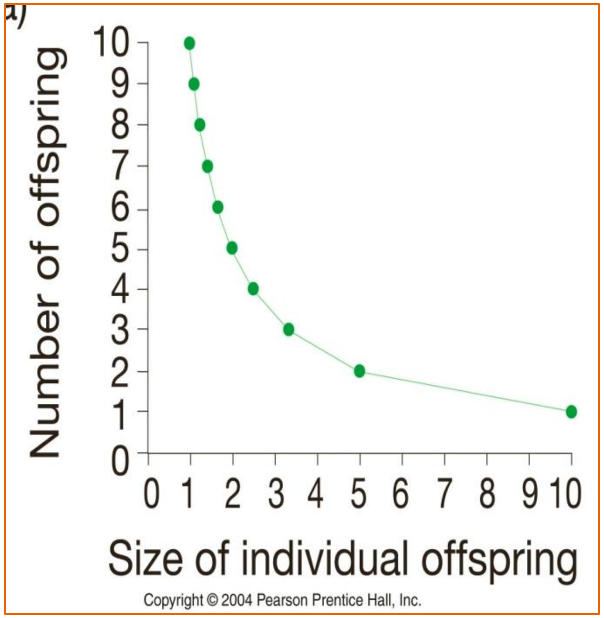
How large should each be?

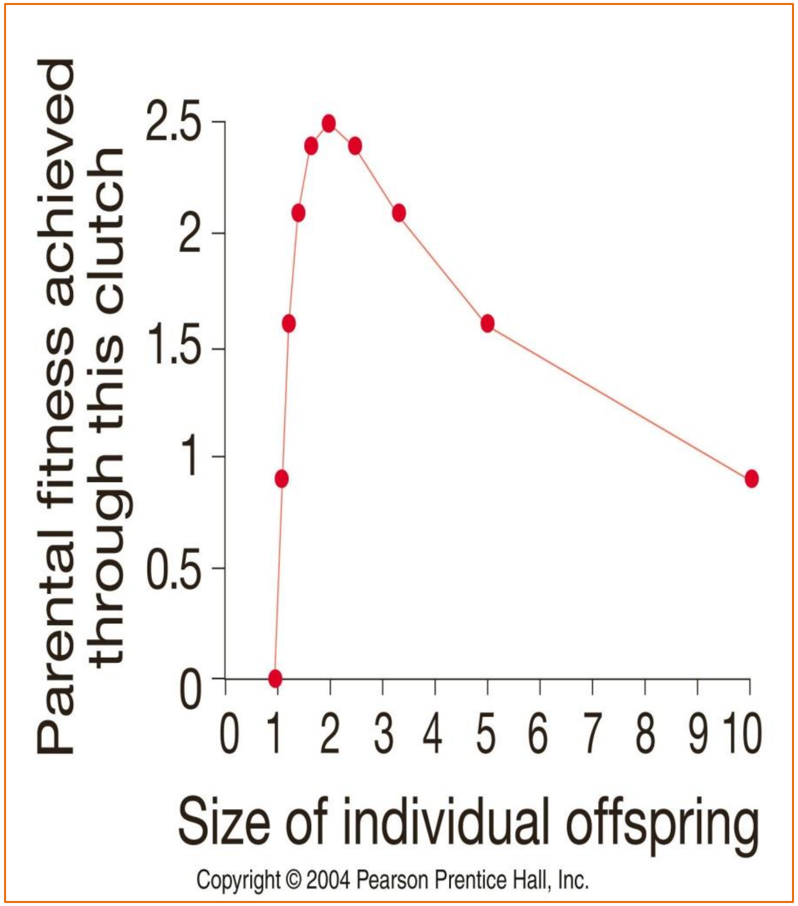
Smith and Fretwell's model

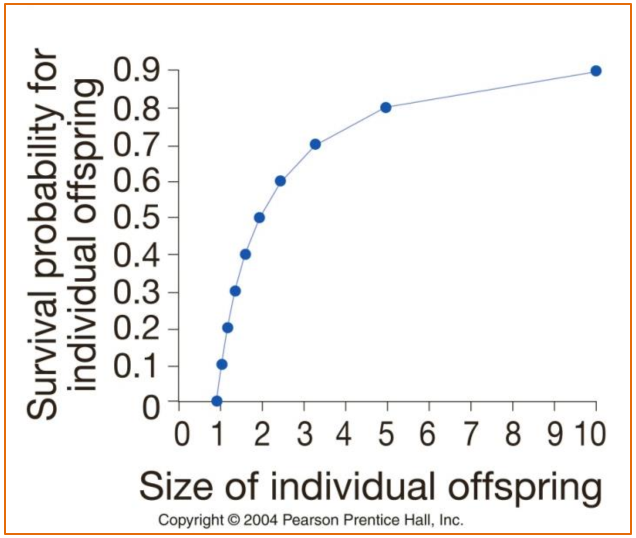
A tradeoff between the number and size of offspring.

That offspring will have a better chance of surviving if they are larger.

Smith and Fretwell's model (1974)







Selection on parents is forced by a fundamental constraint to strike a balance between the number and size of offspring.

Trade-offs due to captive breeding

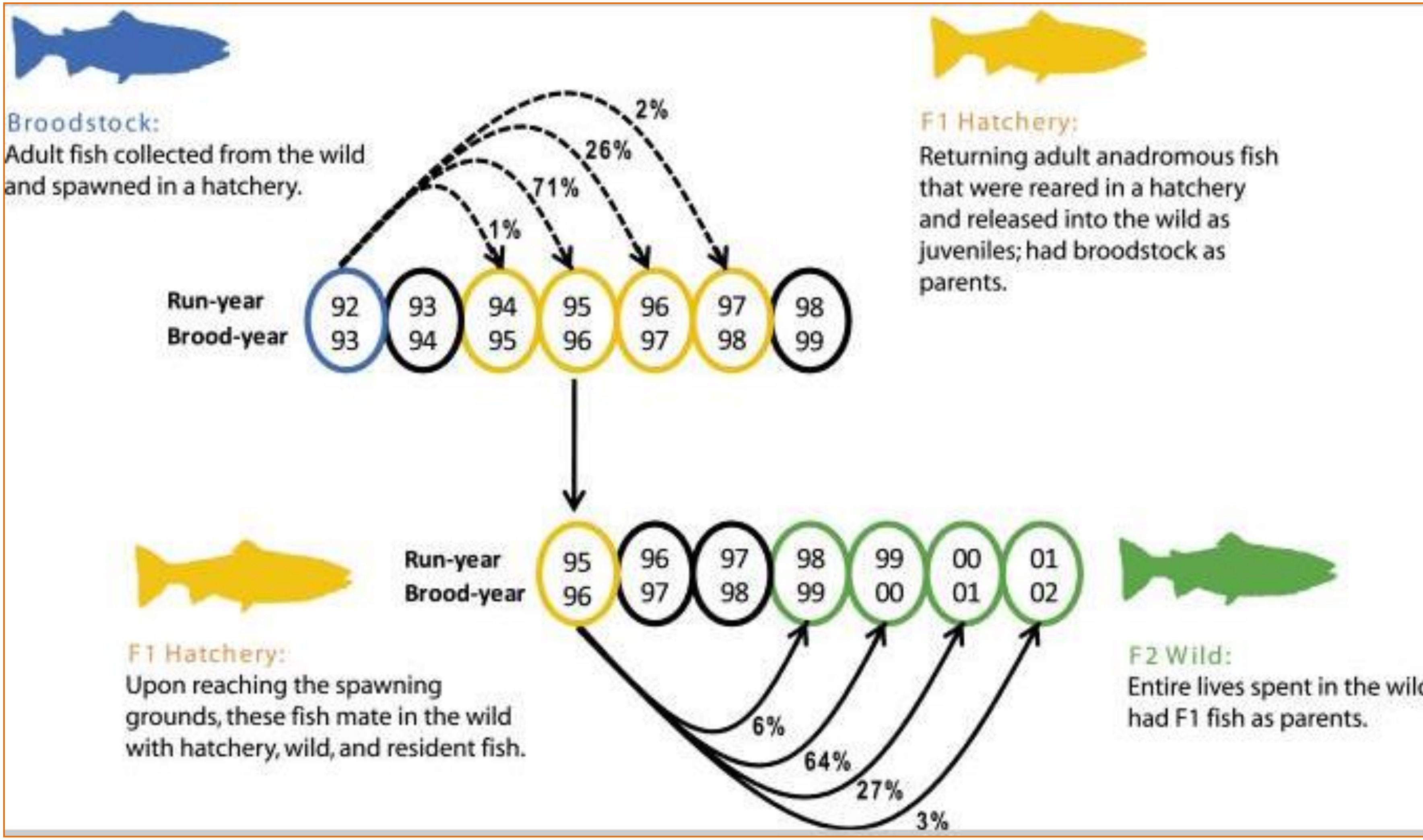
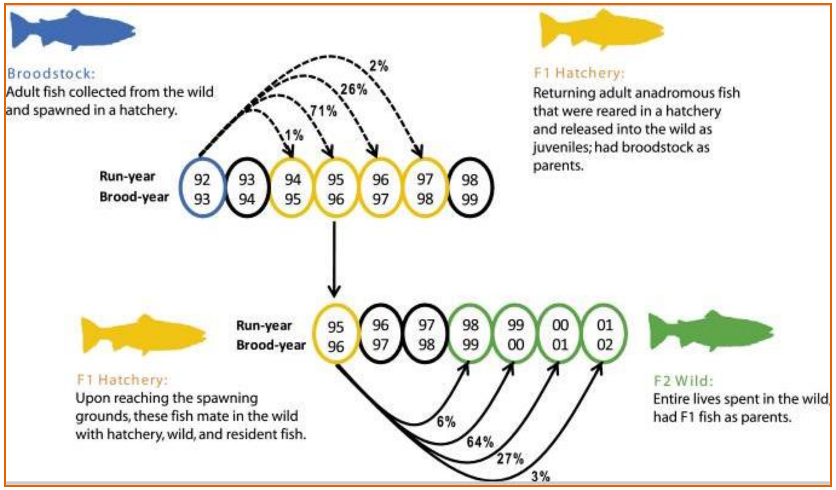


Illustration of the experiment design (Christie et al 2012)

Trade-offs due to captive breeding



Steelhead from the Hood River in Oregon, USA.

Declared as threatened under the US Endangered Species Act.

Fish with trait values associated with success in the captive environment produced large numbers of hatchery-reared F1 offspring that survived to become reproductively mature adults. However, the F1 fish from those large families had low per capita reproductive success in the wild.

This tradeoff is consistent with a rapid response to domestication selection.

Phenotypic plasticity in breeding

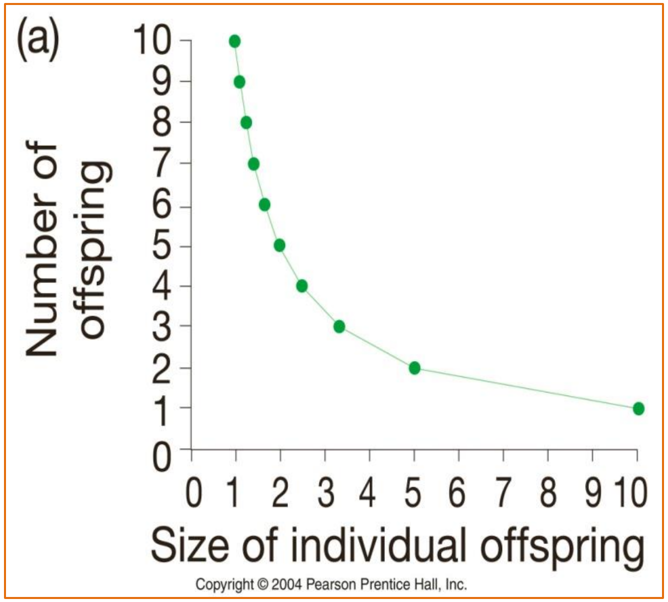
Stator limbatus

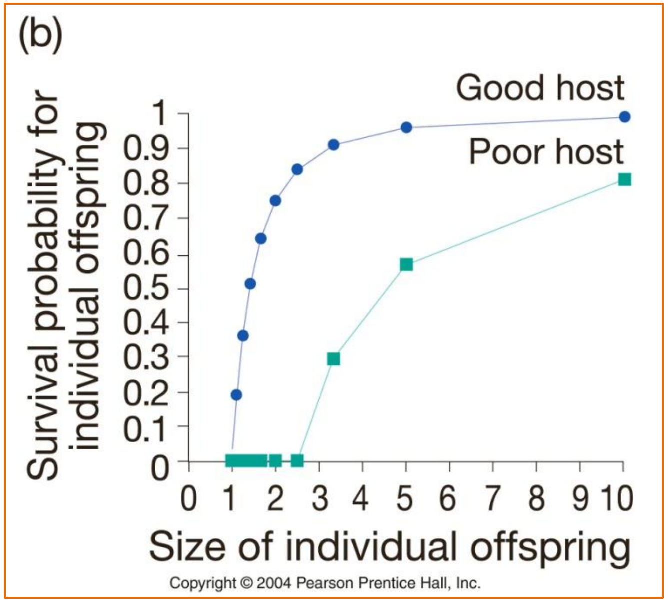
Cercidium floridum

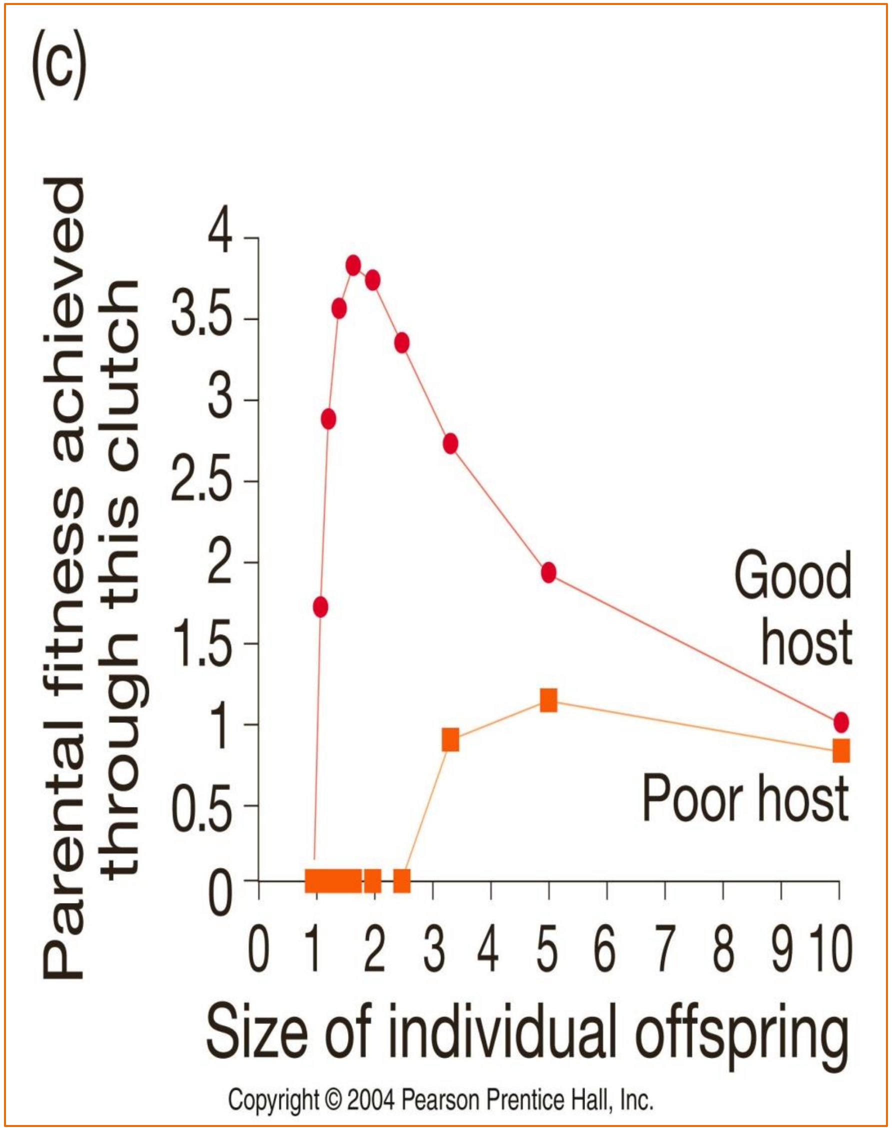
Acacia greggii

Fox et al 1997. The seed beetle females lay larger and fewer eggs on *C. floridium* than *A. greggii*. Larval mortality on *C. floridum* is higher. The females readjust egg size when switched between hosts, suggesting that egg size is an adaptively plastic character in *S. limbatus*.

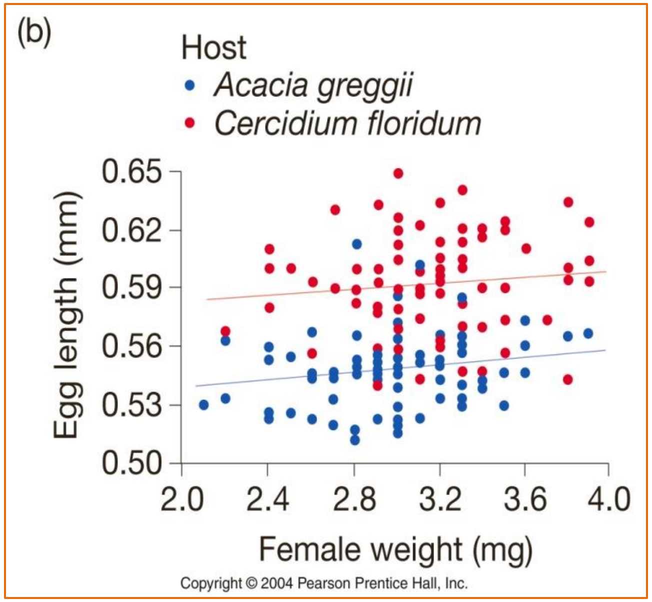
Phenotypic plasticity in breeding

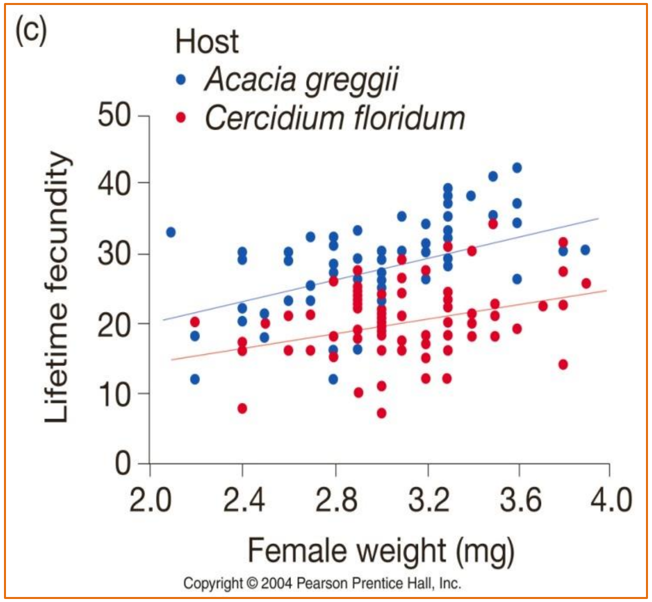


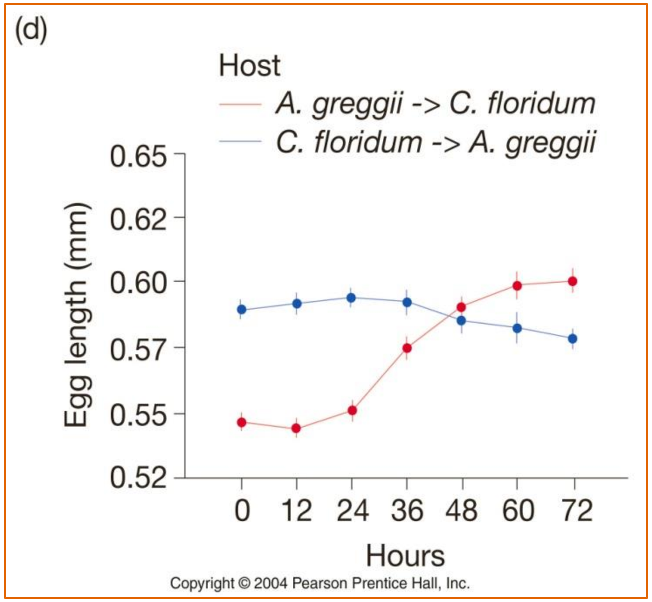


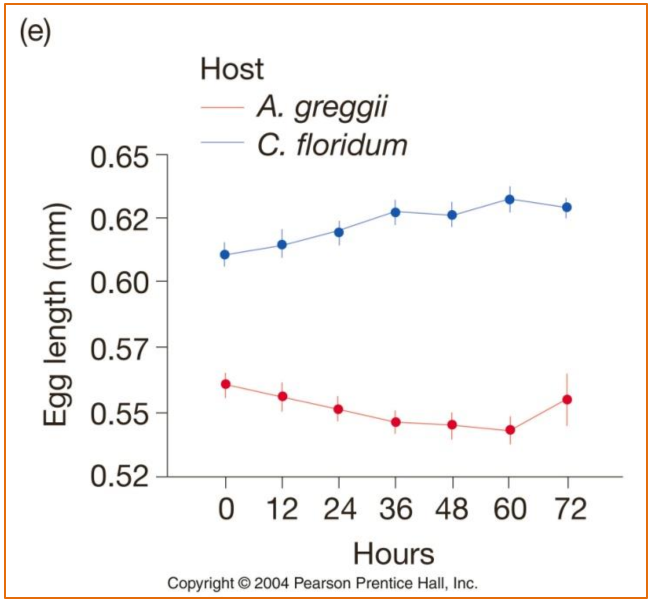


Phenotypic plasticity in breeding









The effect of predation

Reznick and Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*).

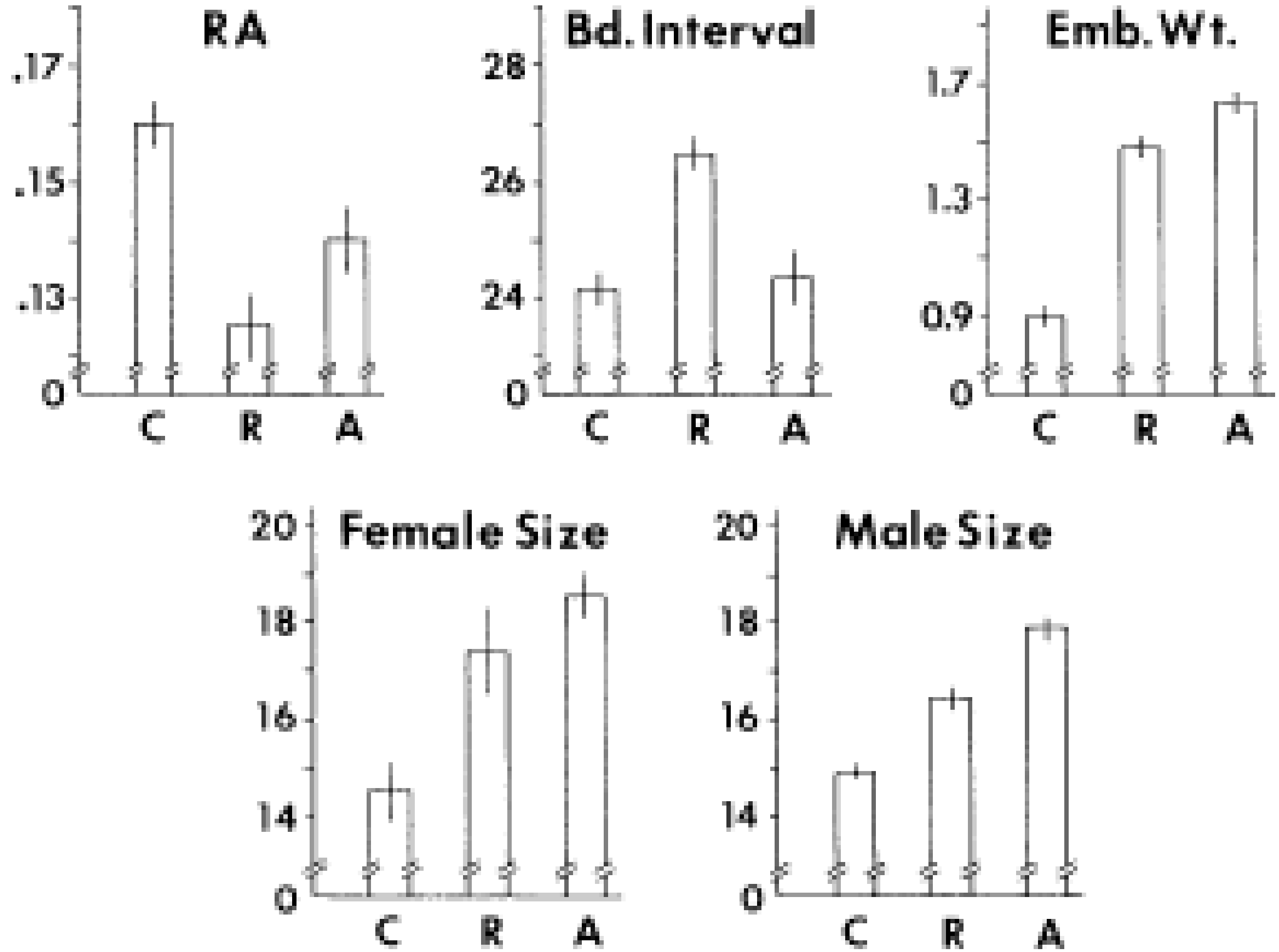
The sites differed in the predator species present and the type of predation

Crenicichla alta (a cichlid), high predation intensity, predominantly on adult guppies

Rivulus hartii (a killifish), moderate predation, predominantly on juveniles

Aequidens pulcher (a killifish), low predation on all size classes

The effect of predation



The effect of predation

The sites where adults were subject to heavy predation by cichlids and juveniles generally escaped predation, that guppies allocated a higher proportion of their body reserves to reproduction, had a shorter interval between broods, produced smaller young and matured at smaller weights than guppies at a site where killifish preyed predominantly on juveniles.

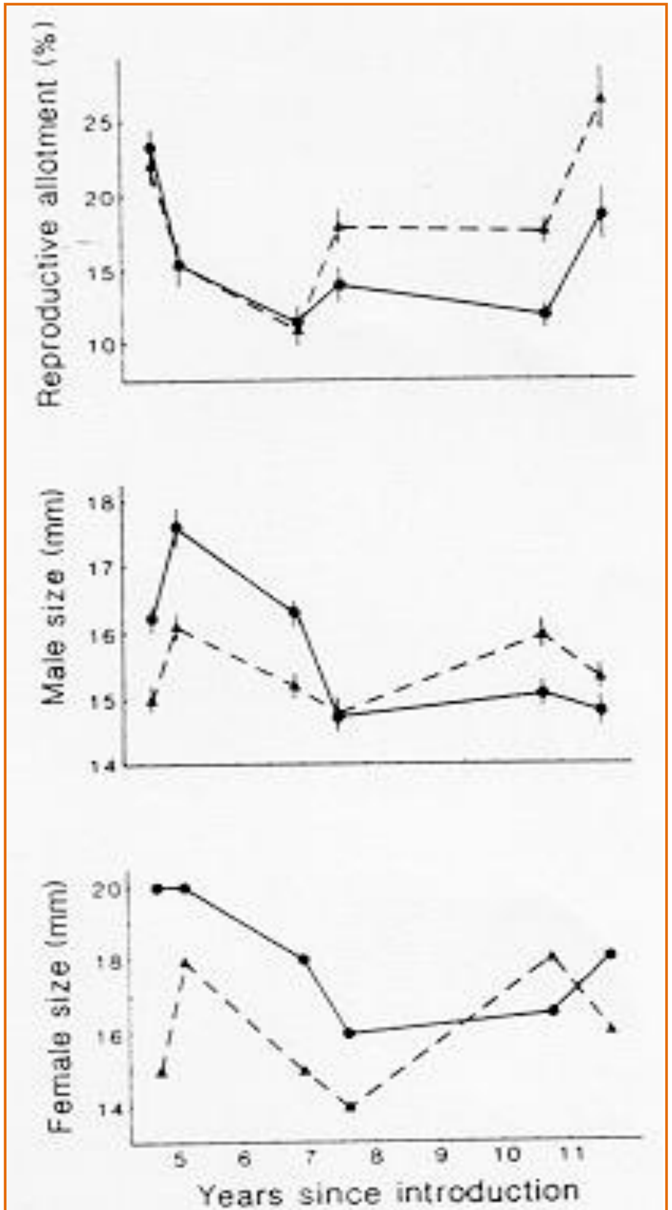
The effect of predation

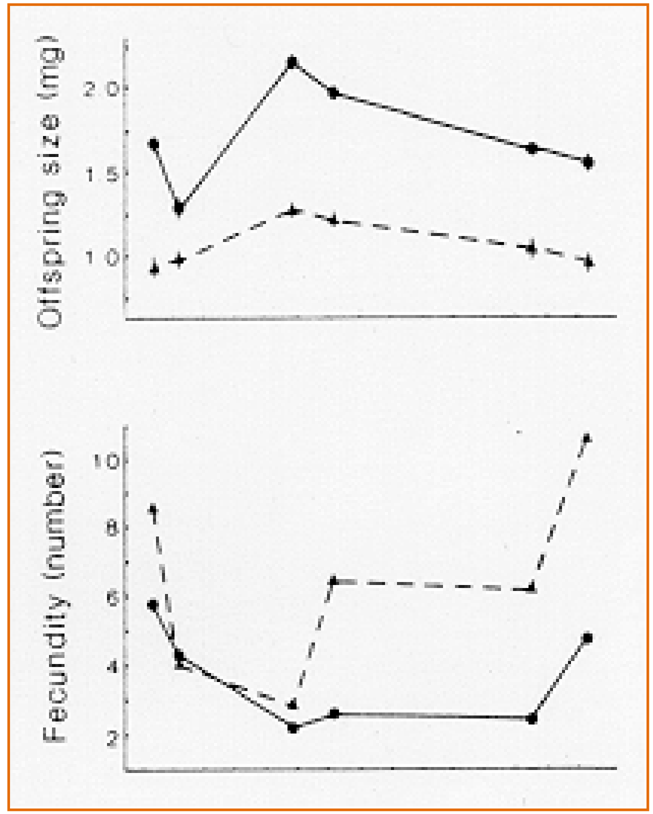
All these traits have high heritabilities which led Reznick and Endler (1982) to speculate that introduction experiments would rapidly produce the optimum phenotype.

Reznick et al (1990) experimentally demonstrated a change in life history by changing the age specific predation against adults to predation against juveniles following an 11 year experiment (30-60 generations).

200 guppies were transplanted in 1976 from a site with Crenicichla to a site on the same river containing Rivulus but no guppies.

The effect of predation





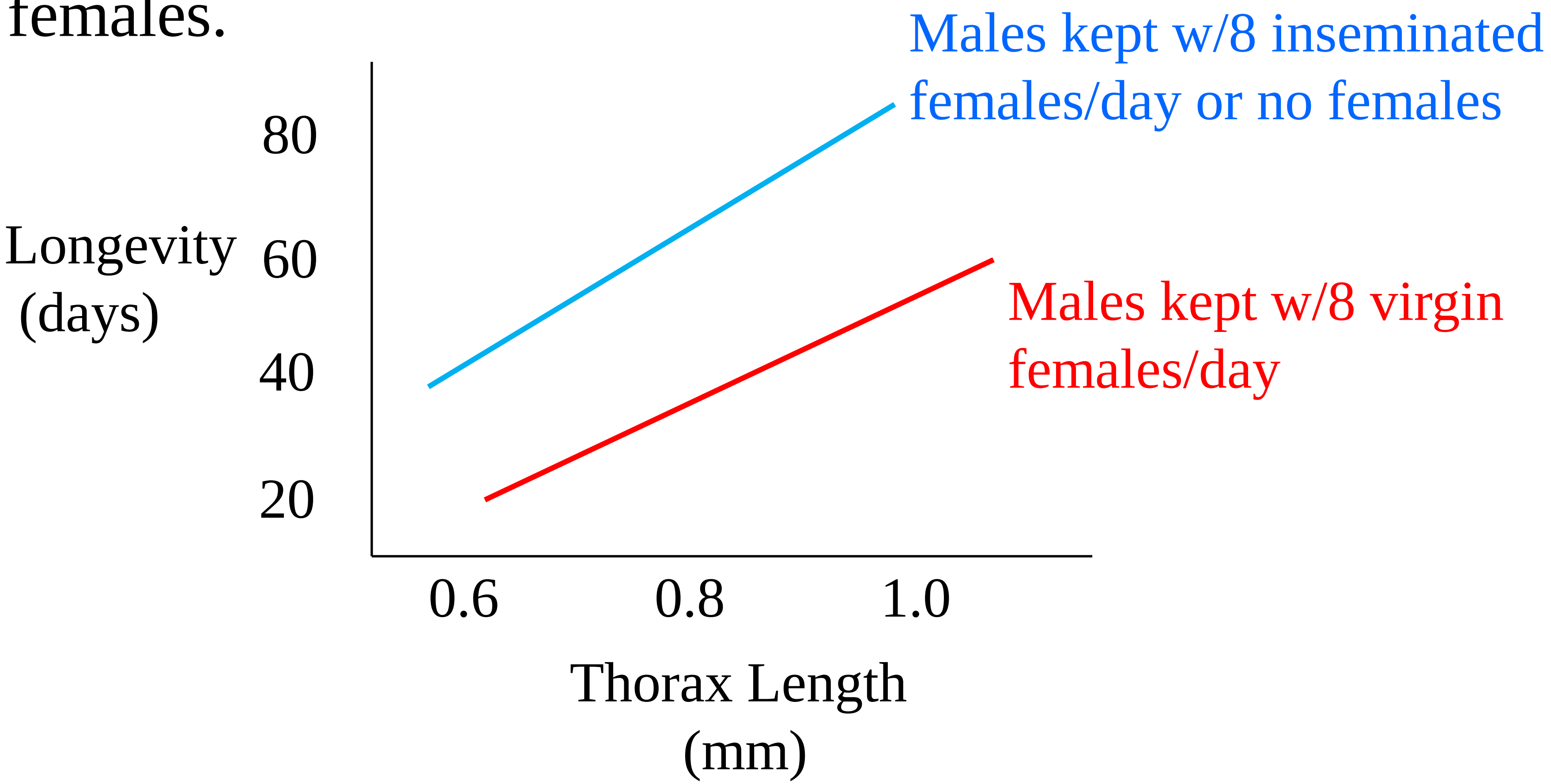
------- CONTROL

_____ INTRODUCTION

This treatment should favor guppies with delayed maturity and decreased reproductive effort, compared to the control site.

Reproduction and longevity

Partridge and Farquhar (1981) showed that male *Drosophilia melanogaster* supplied with virgin females have lower longevity than males kept without access to females.



Reproduction and growth

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In *Armadillidium vulgare*, a grassland dwelling isopod, reproductive females grow much less than non-reproductive females because allocation of energy to reproduction takes place at the expense of allocation of energy to growth.

	Female Size		
	20-39	40-59	60-99 mg
GROWTH RATES (weight increase @ ecdysis)			
Non-reproductive	3.91	3.13	3.10
Gravid	0.96	1.01	0.46

Reproduction and growth

Inflorescence production is inversely correlated with ramet production in the water hyacinth.

The flowering population exhibited a 22% lower saturation density than the non-flowering population and took 85 days in contrast to 35 days for the vegetative population to reach saturation (Watson 1984).

Body size

Age at maturity

Resources

Predation pressure

Number and size of offspring

Genetic constraints

Evolutionary constraints

Life, in ecological terms

$$N_{now} = N_{then} + B - D + I - E$$

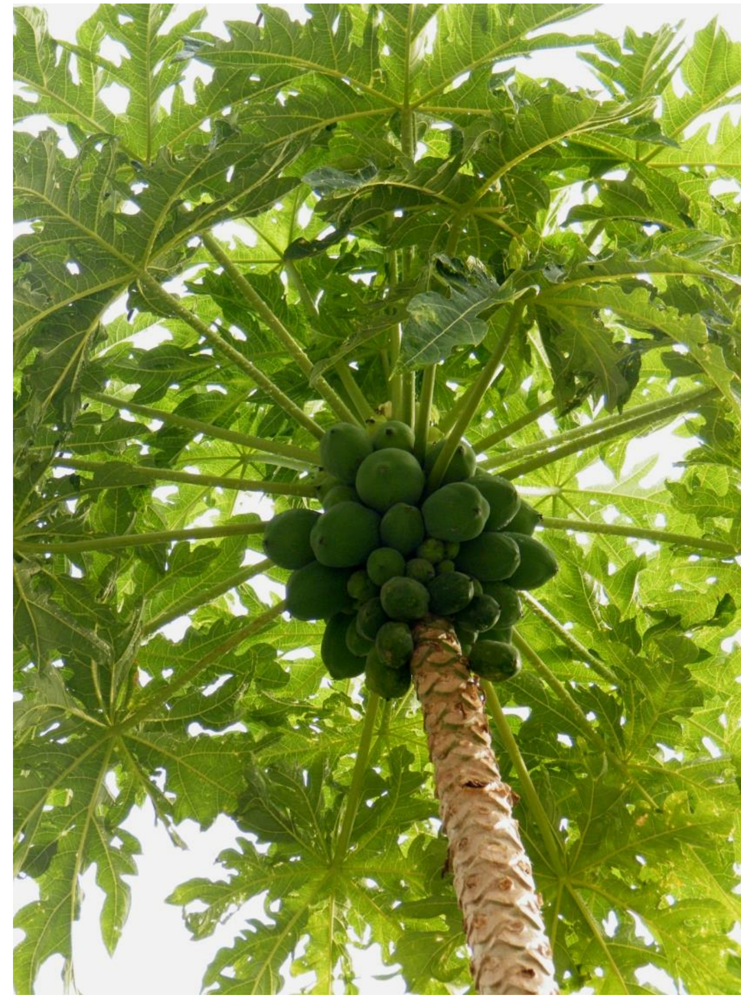
Ecologists aim to describe, explain and understand the distribution and abundance of organisms.

Number of individuals
Distribution of individuals
Demographic processes
Environmental factors

What is an individual?

Individuals are not identical.

They differ in their life cycle stages, quality and condition.



Organisms can be unitary or modular.

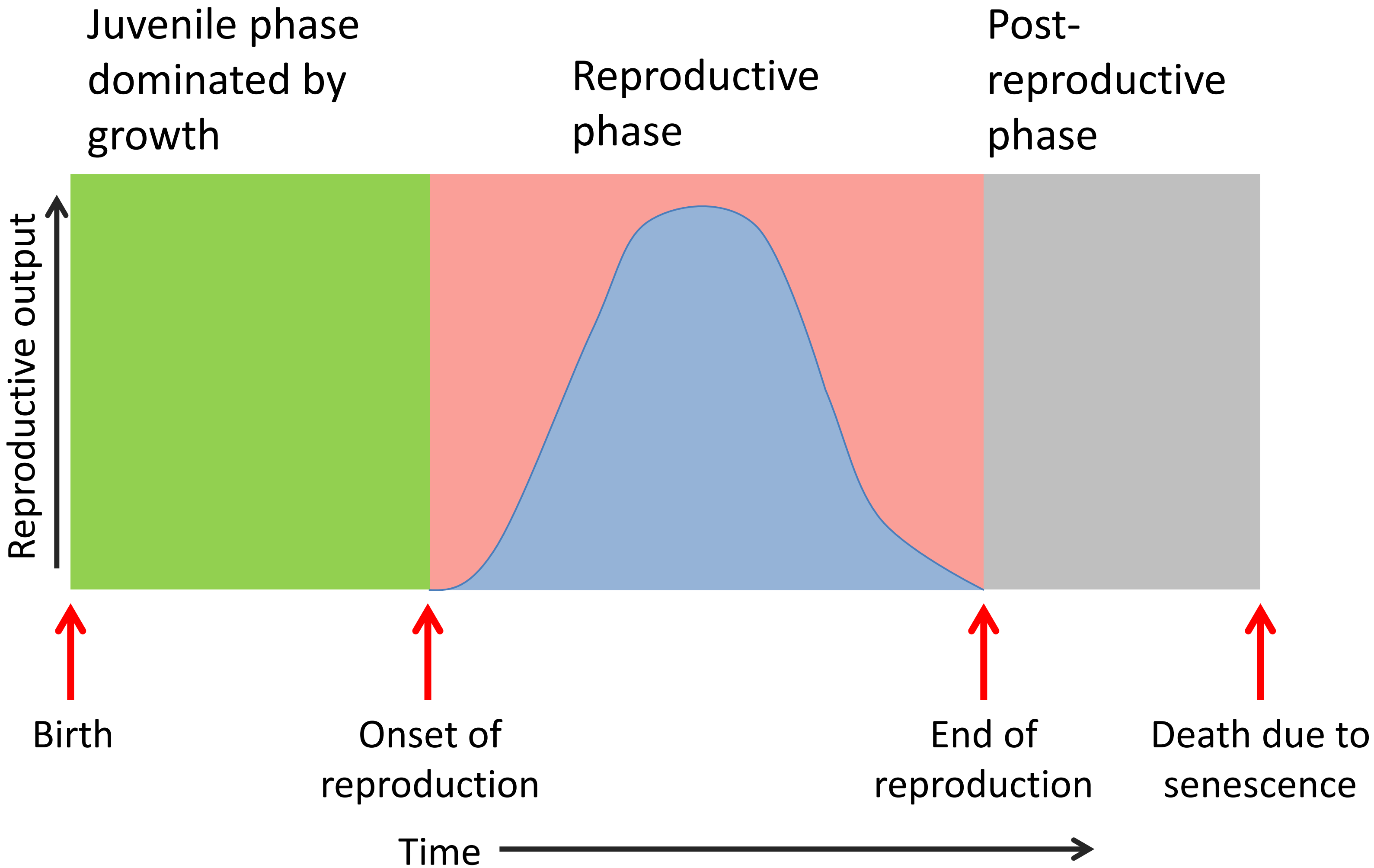
What is a population?

Individuals of a species inhabiting a certain area.

Population size can be estimated using various methods.

Birth and death rates are important factors determining population size.

Life cycles



A typical life cycle outline of a unitary organism

Life cycles

Semelparous (monocarpic):

Individuals have a single distinct period of reproduction.

Cease to grow before reproduction sets in.

Invest little or nothing in survival to future reproductive events.

Die soon after reproducing.

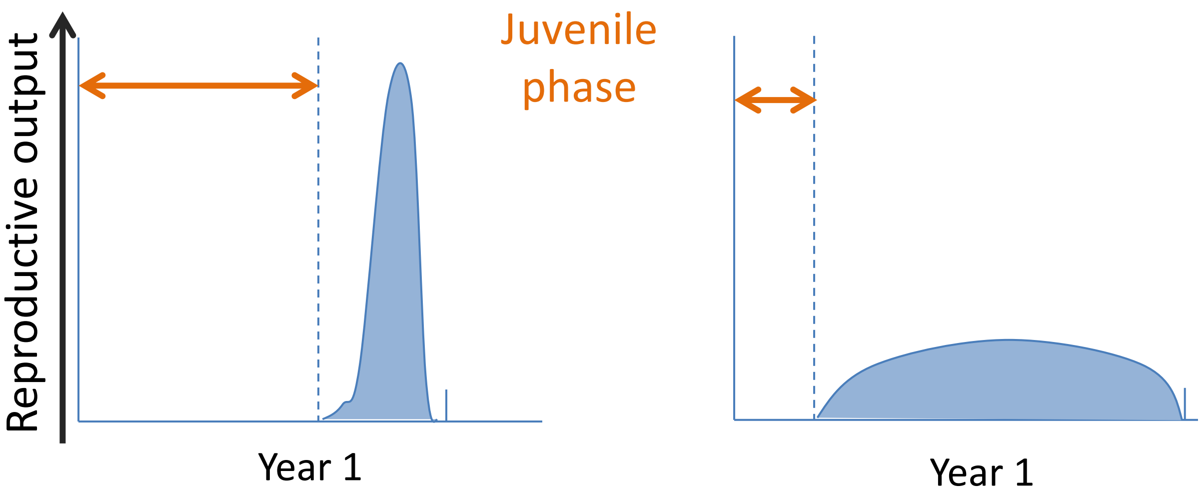
Iteroparous (polycarpic):

Individuals have multiple reproductive events.

During each period of reproductive activity the individual invests in future survival and even growth.

Semelparous and Iteroparous

Many but not all annual plants are semelparous.



Question: (i) Plot similar graphs for an iteroparous annual species, a semelparous species living longer than one year and a long lived species with continuous breeding.

(ii) Can you find examples for each category?

Semelparous and Iteroparous

Many long-lived semelparous species show marked seasonality.

Mating or flowering is commonly triggered by the length of the photoperiod – brood development occurs during high resource abundance.

Generations overlap and individuals of different ages breed simultaneously.

In equatorial climates we find species that are in fruit and flower round the year and animals that breed continuously.

Semelparous and Iteroparous

The Pacific salmon is semelparous. They spawn in the river, travel to the sea and return to breed in the river in 2-5 years' time. They lay their eggs and die.

The bet hedging model

Increasing environmental variability and unpredictability should favour **iteroparity over semelparity.**

Limiting reproductive output to a single episode is particularly risky in an unpredictable environment.

But annuals and biennials are typically found in unpredictable habitats like deserts or disturbed sites.

How do semelparous species solve this problem?

The bet hedging model

In annual plants strong seed dormancy provides considerable variation in generation time within each cohort.

	No Dormancy or Conditional		**Full Dormancy**		
	#	**%**	**#**	**%**	**#sp.**
Annuals	43	0.49	45	0.51	88
Monocarpic perennials	13	0.81	3	0.19	16
Polycarpic perennials	32	0.68	15	0.32	47

In non-annual plants there is variation in post-germination maturation time, which can be genetic or caused due to microenvironmental variation.

The reproductive effort model

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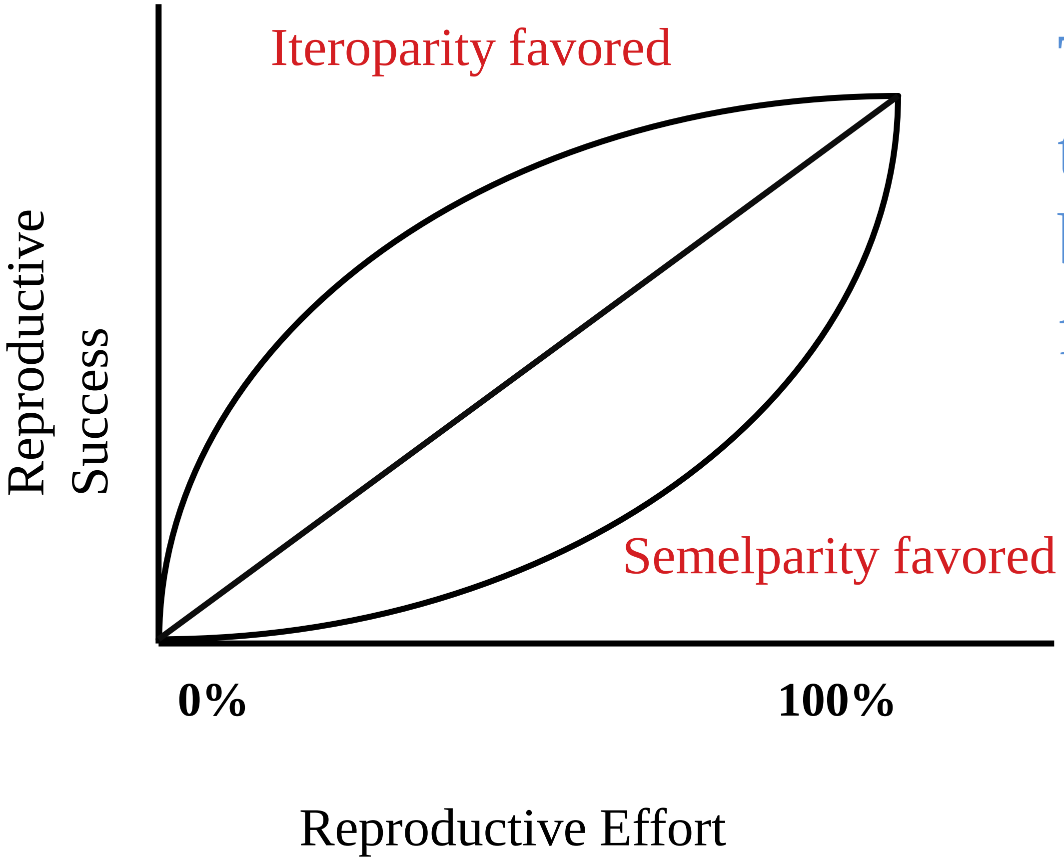
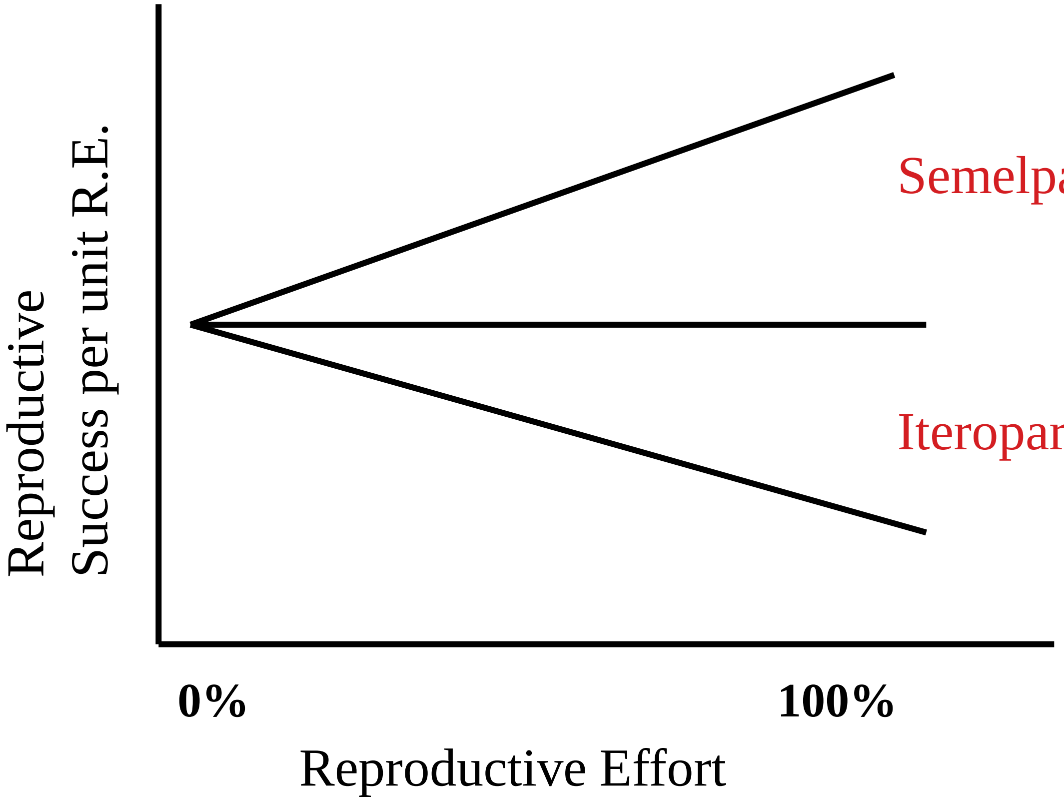


This model considers the relationship between present and future reproduction.

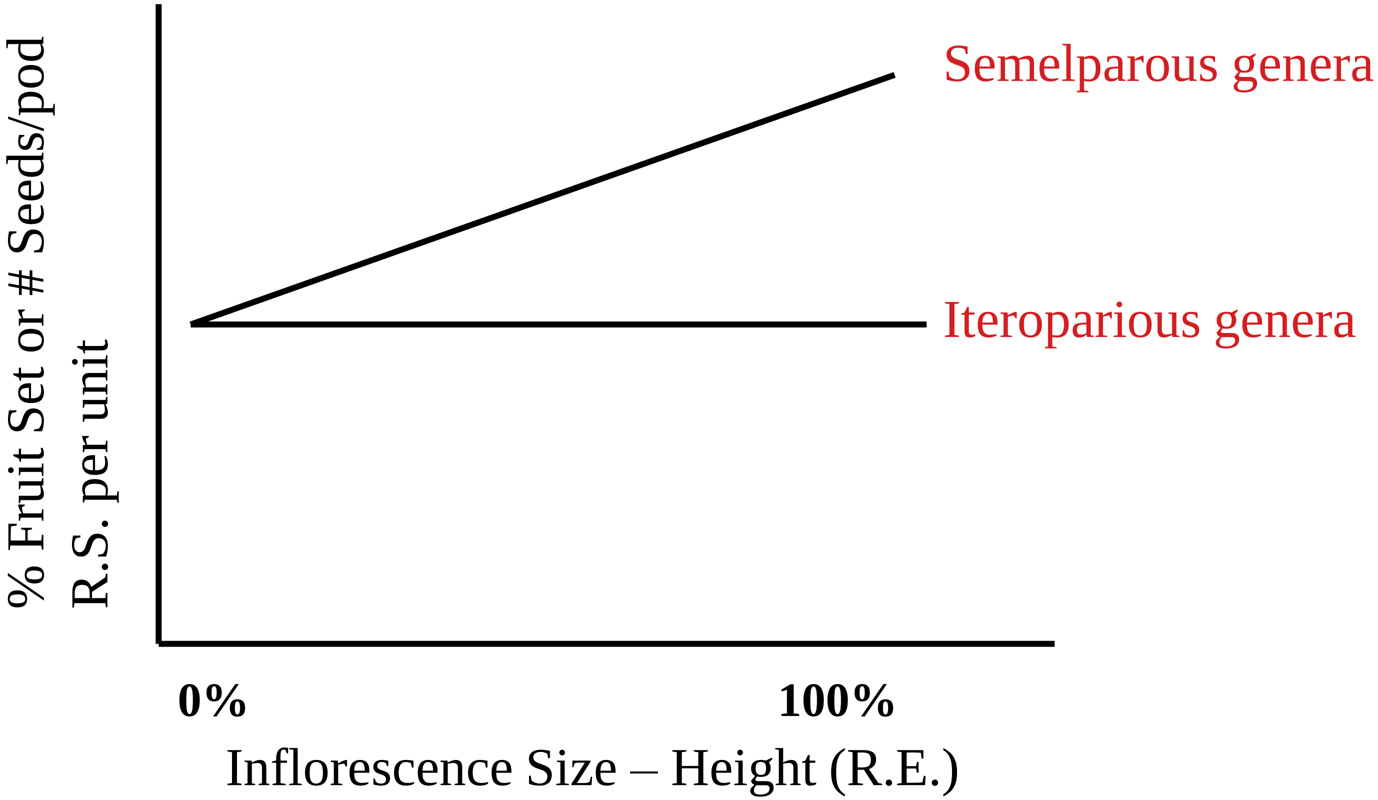
Semelparity will be preferred over iteroparity when greater benefits of reproduction come at higher reproductive effort.

The reproductive effort model



When there is a positive correlation between reproductive effort and reproductive success per unit reproductive effort, semelparity will be favored, but when this relationship is absent or negative, iteroparity will be favored.

The reproductive effort model



Interspecific comparisons of field data from three different genera *Yucca*, *Agave*, and *Lobelia* have all shown this pattern

Fitness as a life history trait

Semelparous life history

$R = LM$

R =number of descendants of an average female after one generation,

L = probability of a female's survival to reproductive age

M = average number of offspring per survivor

Iteroparous life history

Sum of the offspring an average female produces at each age, weighted by the probability that a female survives to that age.

Fitness as a life history trait

x = age, l_x = the probability of survival to age x (proportion of eggs or newborns that survive to age x), and m_x = average fecundity (number of eggs or newborns) at age x.

$$R = \Sigma l_x m_x$$

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
$\sum = R$			4

Because trait should maximize fitness, organisms should ideally have evolved greater fecundity, longer life, earlier maturation….

Constraints:

Phylogenetic

Physiological - Genetic

Phylogenetic constraints

Evolution has enforced upon each lineage certain features that limit variation in its life history characters.

Adult insects do not grow and hence a female cannot accommodate more eggs with age.

Adult silkworm moths and some other insect groups lack functional mouthparts, so their fecundity is limited by the resources they stored when they fed as larvae.

In Procelariiformes (Albatross, Petrels)- a single egg is laid at a time.

Such lineages cannot rapidly evolve in response to environmental selection pressure.

Genetic constraints

Either lack of *Genetic Variation* or *Genetic Correlation*.

Generally Life History traits display polygenic, additive genetic variation.

High rate of origin of genetic variation by mutation on traits e.g. survival and fecundity balances strong selection pressure.

Negative Genetic correlation between traits: Genotypes may display a negative relationship between fecundity and subsequent survival if they all acquire the same amount of energy but differ in allocation to reproduction and maintenance.

Positive Correlation between reproduction and survival Genetic variation in amount of resource harvest.

Physiological constraints

Trade offs, whereby the advantage of a change in a character is correlated with a disadvantage in other respects.

Reproductive activities of animals often increase their risk of predation, so there is a **trade-off between reproduction and survival**.

Courtship calls of male tungara frogs attract both female frogs and predatory bats

Detecting trade-offs

1. Correlations between the means of two or more traits in different populations or species can strongly suggest a trade-off.

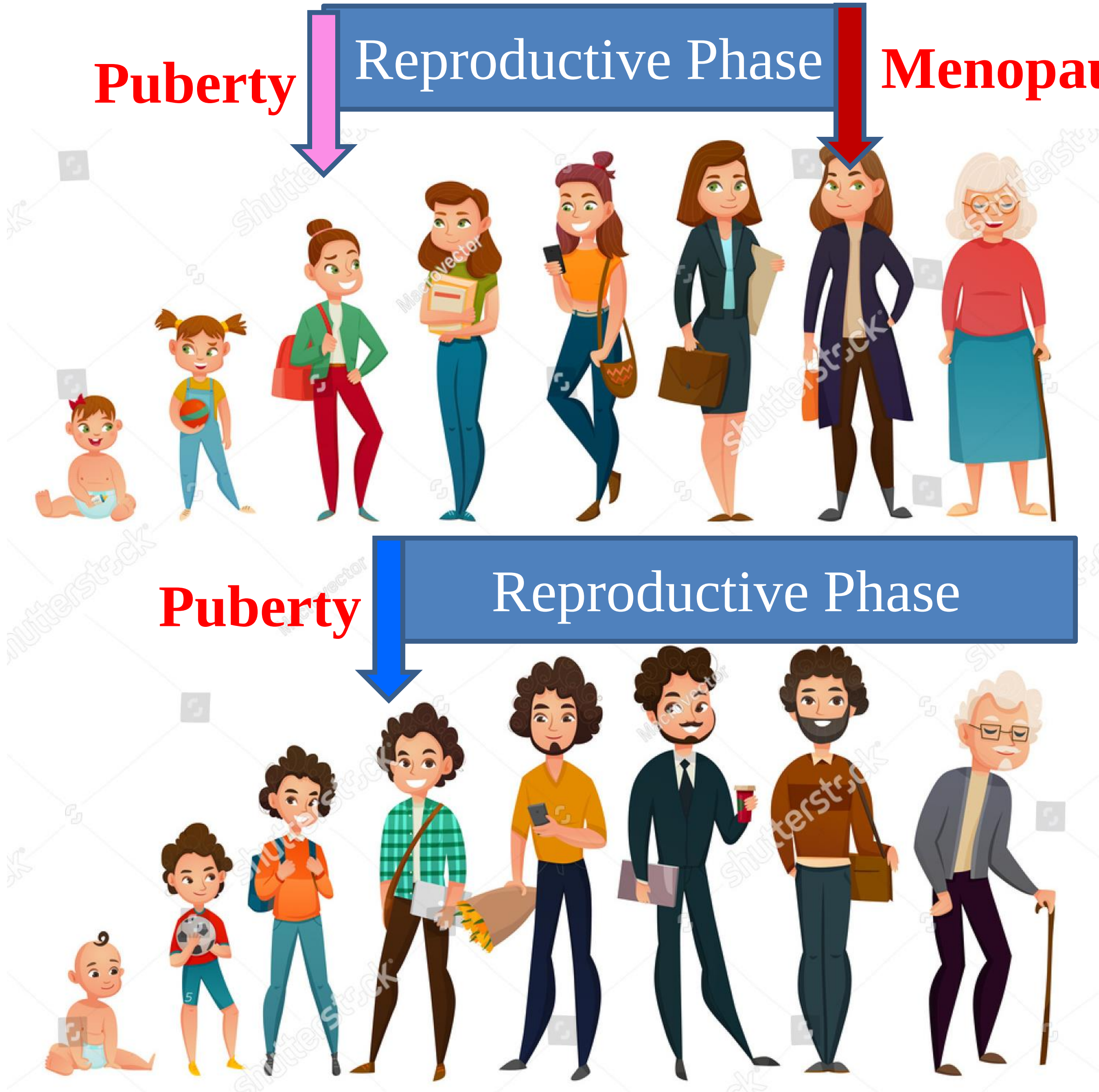
2. Correlated responses to artificial or natural selection
   Imposing selection on one trait and determining if there is correlated change in other trait

3. Measuring one trait and determining effect on another trait. Altering the number of eggs can affect proportion of young that fledge and subsequent survival and reproduction of parents.

The Human Story

Can you plot the graph depicting the reproductive output for humans?

The Human Story



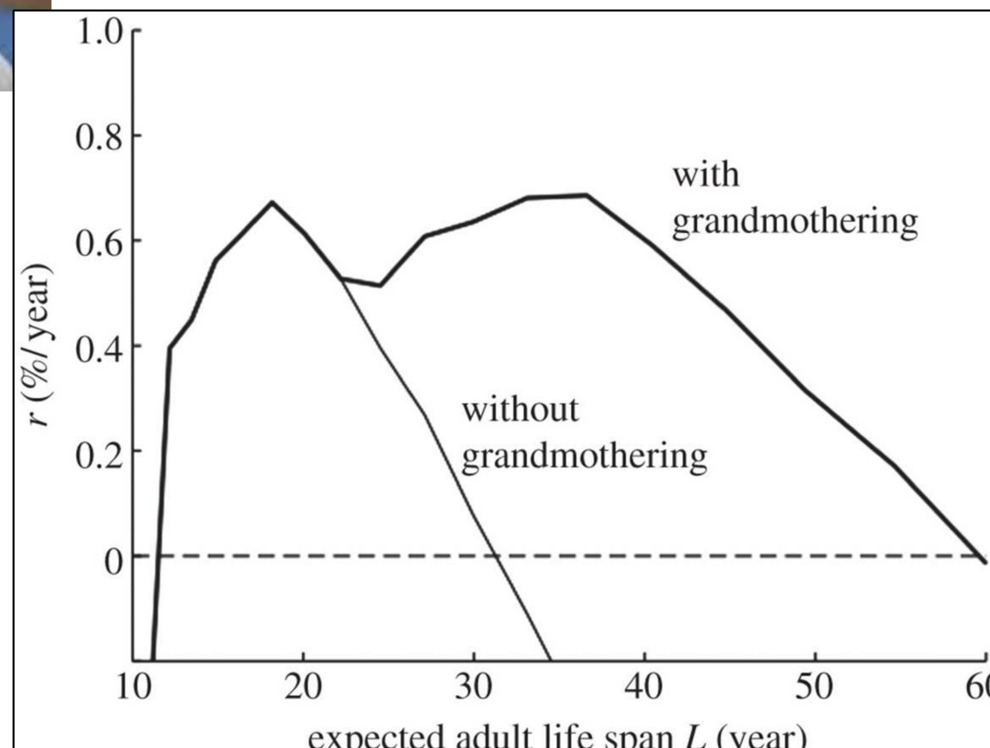
WHY menopause?

Menopause is equivalent to genetic death

The Grandmother Hypothesis

Help from grandmothers enables mothers to have more children.

Women who live longer have more grandchildren



The Grandmother Hypothesis

Genus Homo → Large cranial capacity → Less matured infant at birth → Period of care required longer

Ecological changes → Expansion of grasslands → Change in foraging habits → Eating of tubers, required digging of dry ground, difficult for juveniles → Introduction of cooking → Increased digestibility of food → Post-weaning nutrition easier → Children with grandmothers could survive better → Women who live longer have more surviving grandchildren → Directional selection on post-menopause survival for women.

The Grandmother Hypothesis

Correlation between children's growth and their mother's and grandmother's work.

Hadza tribe – Tanzania: modern day hunter-gatherer society

[Hadza: The Roots of Equality (hadzaexhibit.org)](hadzaexhibit.org)

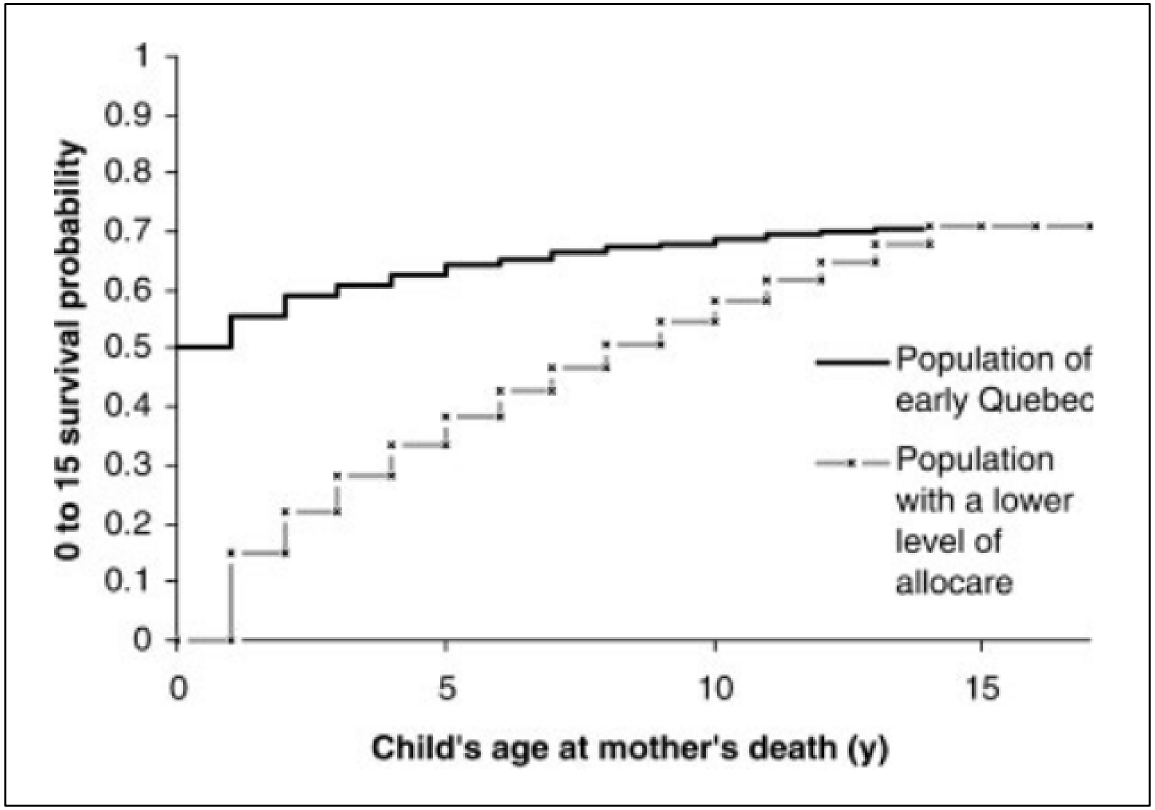
The Patriarch Hypothesis

Males became capable of maintaining high status → reproductive access beyond their peak physical condition → selection favored the extension of maximum life span in males. The relevant genes were not on the Y chromosome → life span increased in females as well.

However, the female reproductive span was constrained by the depletion of viable oocytes, which resulted in menopause.

The Mother Hypothesis

Menopause evolved to avoid higher reproductive-mediated mortality risk in late-life and ensure the survival of existing offspring.



Why Menopause?

Not enough studies to choose one of the possible options.

The grandmother hypothesis is most popular.

In Killer whales, the only other species with a long post-reproductive lifespan for females, support for the grandmother hypothesis has been documented.