Chapter 14.

THE EVOLUTION OF LIFE HISTORIES

Fitness has several major components: survival, female fecundity and male mating success.

- **Simultaneous hermaphrodites** have both male and female sexual functions at the same time.
- **Sequential hermaphrodites** develop first as one sex and later switch to another sex.
- **Parthenogenesis** is the development of an organism from an unfertilized egg.

**Life history** refers to the probability of survival and reproductive success of an organism. The key events in the life of an organism that involve growth, reproduction and survival.

Examples of some major life history characteristics include:

- Age at first reproductive event
- Reproductive lifespan and aging
- Number and size of offspring

**INDIVIDUAL SELECTION AND GROUP SELECTION**

The good of the species does not affect the course of selection among individuals.

The components of fitness (differences in fecundity, and life span) must have evolved at least partly by natural selection.

Selection among populations is weaker than selection among individuals.

Life history traits are components of the individual’s fitness.

The possibility of a species’ future extinction is irrelevant to, and cannot affect, the course of natural selection among individuals.

A mutation that would increase an individual’s fitness would become fixed.

The level of mortality is a consequence of the level of fecundity in a population, because density-dependent factors such as limited food and other resources regulate most populations.

**MODELING OPTIMAL PHENOTYPES**

The **Optimality Theory** is also called the **Optimization Theory** in evolutionary biology.

- Note: It is different from the Optimality Theory in grammar and phonology.

*Optimization models help us to test our insight into the biological constraints that influence the outcome of evolution. They serve to improve our understanding about adaptations, rather than to demonstrate that natural selection produces optimal solutions.*


This theory helps to understand different types of life history adaptations: what stated of some characters, among a specified set of plausible states (strategies) would maximize individual fitness, subject to specified constraints.
The Optimality Theory assumes that sufficient genetic variation has been available for natural selection to shape a feature

- It ignores the history of genetic changes.
- It looks only at the future, the expected outcomes.

**Criticism**: constraints such as limited genetic variation or genetic correlations may prevent the attainment of an optimum.

**Defenders reply**: this approach does not assume that organisms are perfectly adapted, but instead aims to understand specific examples of adaptations.

General optimal models provide qualitative insights into the kinds of broad solutions to adaptive problems that might be expected to evolve.

- See the example of surface to volume relationship on page 372.

An **evolutionarily stable strategy** is such that, if all the members of a population adopt it, the no mutant strategy could invade under the influence of natural selection.

**LIFE HISTORY TRAITS AS COMPONENTS OF FITNESS**

Among the most important components of fitness are:

1. Survival to and through the reproductive ages.
2. The number of offspring of females (fecundity)
3. The number of offspring a male fathers.

**FEMALE FECUNDITY, SEMELPARITY AND ITEROPARITY**

**Semelparous life history**: the female reproduces once and then dies.

Reproductive success in this case is the number of descendants of an average female after one generation: \( R = LM \)

- \( R \) = the product of the probability of a female’s survival to reproductive age.
- \( L \) = the probability of a female’s survival to reproductive age.
- \( M \) = average number of offspring per survivor

**Iteroparous life history**: the female reproduces more than once in her lifetime.

- See example on pages 374 and 375

A genotype with higher \( R \), will increase faster and have higher fitness.

If genotypes differ in the length of a generation, their fitness can be compared only by their increase per unit time, not per generation.

The per capita rate of population increase per unit time is denoted \( r \).

If the population starts with \( N_0 \) individuals, its size after \( t \) time units will be \( N = N_0 e^{rt} \).
AGE STRUCTURE AND REPRODUCTIVE SUCCESS

Offspring produced at an early age increase fitness more because they contribute more to population.

Reproduction at an early age contributes more to the rate of population growth than an equal production of offspring later in life.

Older females are less likely to be alive to reproduce.

TRADE-OFFS

Various constraints will prevent organisms to evolve ever greater fecundity, ever longer life, and ever earlier maturation.

- **Trade-offs** are the linkages between traits that constrain the simultaneous evolution of two or more traits

  - Some of the most commonly studied trade-offs include:
    - Survival vs. reproduction
    - Current vs. future reproduction
    - Reproduction and growth
    - Reproduction and condition
    - Quality and quantity of offspring

**Phylogenetic constraints** are features that have accumulated in the evolutionary history of the species that resist evolutionary change, e.g. birds in the order Procellariiformes lay only one single egg, while other groups lay clutches of eggs.

**Genetic or physiological constraints** occur when the advantage of a trait is correlated with a disadvantage in other respects.

  - Linked traits limit variation
  - Allocation of resources to one aspect of the organisms but not to all aspects.

**Antagonistic pleiotropy** can be the result physiological trade-offs, wherein genotypes show an inverse relationship between different components of fitness.

  - Allocation trade-off: cost of reproduction decreases survival of the parents.
  - Organisms have a limited amount of energy and must divided among several functions.
  - There is a trade-off between fecundity, growth and survivorship in its life history strategy.

“In laboratory and field experiments on bivalves, cladocerans, insects, and mammals, allocation to maintenance or storage was found to take precedence over allocation to reproduction under nutrient-poor or stressful conditions (Rogowitz 1996, Perrin et al. 1990, Boggs & Ross 1993, Jokela & Mutikainen 1995, Zera et al. 1998).” - Anthony J. Zera and Lawrence G. Harshman. *Annu. Rev. Ecol. Syst.* 2001. 32:95–126
Recommended article on life-history trade-offs:
http://www.public.iastate.edu/~nvalenzu/EEOB514/Readings/3-
NonMandatoryPapers/Zera&Harshman2001_LHTradeoffPhysiol.pdf

Detection of trade-offs:

1. Correlations between the means of two or more traits in different populations or species could point at a trade-off.

Example:
"Mutations often have consequences that vary across individuals. Here, we show that the stimulation of a stress response can reduce mutation penetrance in Caenorhabditis elegans. Moreover, this induced mutation buffering varies across isogenic individuals because of interindividual differences in stress signaling. This variation has important consequences in wild-type animals, producing some individuals with higher stress resistance but lower reproductive fitness and other individuals with lower stress resistance and higher reproductive fitness. This may be beneficial in an unpredictable environment, acting as a “bet-hedging” strategy to diversify risk. These results illustrate how transient environmental stimuli can induce protection against mutations, how environmental responses can underlie variable mutation buffering, and how a fitness trade-off may make variation in stress signaling advantageous."

Fitness Trade-Offs and Environmentally Induced Mutation Buffering in Isogenic C. elegans

2. Phenotypic or genetic correlations between traits with populations.
Example:
Law and colleagues (1979) investigated the number of inflorescences and vegetative growth in two seasons using the grass Poa annua. See page 378.

3. Correlated response to artificial and natural selection.

4. Experimental manipulation of one trait and observation of the effect on other traits.

THE EVOLUTION OF LIFE HISTORY TRAITS

1. LIFE SPAN AND SENESCENCE

Most organisms in which germ cells are distinct from somatic tissues undergo physiological degeneration with age. This process is called senescence.

- The shortening of the telomeres has been proposed as the cause of this phenomenon.

Senescence differs among species.

There are two related hypotheses about the evolution of senescence and life span.

- Deleterious mutations that affect later age classes accumulate in populations at a higher frequency than those that affect earlier age classes because selection against them is weak.
• Antagonistic pleiotropy or genetic trade-offs. Because of the greater contribution of earlier age classes to fitness, an allele that is advantageous early in life, such as one that increases reproductive effort, has a selective advantage even if it is deleterious later in life, perhaps because it reduces the allocation of energy and materials to maintenance, repair and defense. That is, senescence may be one the costs of reproduction.

There is a strong experimental evidence in favor of the second hypothesis.

The role of energetics in life history trade-offs is not well understood yet.

“Birds have the highest core body temperature of any endotherm (Nagy 1987) and flying birds have size constraints that presumably limit the amount of energy storage (Calder 1984). Thus, it would appear that energetics must play an important role in shaping bird life histories (Walsberg 1983, Paladino 1989, McNab 1997). Birds expend relatively high levels of energy during reproduction and thermoregulation (Weiner 1992). Energy constraints, which can arise from the competing costs of reproduction, thermoregulation, growth, energy assimilation, and energy assimilation capacity (Karasov 1986, Weiner 1992, Konarzewski 1995, Jackson & Diamond 1996), could be integral to life history evolution.” Anthony J. Zera and Lawrence G. Harshman. Annu. Rev. Ecol. Syst. 2001,32:95-126.

2. AGE SCHEDULES OF REPRODUCTION

Reproducing at an early age may increase the risk of death, decrease growth, or decrease subsequent fecundity so as to lower r compared to with what it would be if reproduction were deferred.

Fecundity is often correlated with body mass in species that grow throughout life, such as many plants and fishes.

In such species, allocating resources to growth, self-maintenance, and self-defense rather than to immediate reproduction is an investment in the much greater fecundity that may be attained later in life.

Mathematical models have shown that repeated reproduction is more likely to evolve if adults have high survival rates from one age class to the next, and if the rate of population increase is low.

The above factor can also help to evolve a genetically longer life span.

Because some resources are used for growth, maintenance and defense, the effort devoted by an iteroparous species to reproduction will be less at each reproductive age than what a semelparous species devotes to reproduction in its single reproductive episode.

As individuals age, the benefit of withholding energy from reproduction declines because the prospects of subsequent reproduction decline. The proportion of energy or other resources devoted to reproduction by iteroparous species should increase with age.

High adult survival rates favor delayed maturation and high reproductive effort later in life.

See D. Reznick’s experiment with guppies in Trinidad, page 380-381.

3. NUMBER AND SIZE OF OFFSPRING.
Everything being equal, a genotype with higher fecundity has higher fitness than one with lower fecundity.

OPTIMAL CLUTCH SIZE

**Optimal clutch size** for a bird is the number of eggs that yields the greatest number of surviving offspring.

The number of surviving offspring from larger broods may be less than the number from more modest clutches because parents are unable to feed larger broods adequately.

- The decrease in offspring survival has proved to be one of several costs of large clutch size in birds.
- Excessively large clutches may also reduce the parents’ subsequent clutch size and survival.

See Timmergen and Daan’s experiment on page 383.

PARENTAL INVESTMENT

**Parental investment** refers to parents’ provision of yolk, endosperm, nourishment, or other forms of parental care.

There is a negative correlation between number and size of offspring.

The female’s reproductive success – number of surviving offspring they leave to the next generation – should be maximized by producing a modest number of offspring that are larger and better equipped for survival.

*The marginal cost of offspring produced is decreasing (each additional offspring is less “expensive” than the average of all previous offspring) and the marginal cost of offspring forgone is increasing. In this situation, the organism only devotes a portion of its resources to reproduction, and uses the rest of its resources on growth and survivorship so that it can reproduce again in the future. Roff, Derek A. (1992). The Evolution of Life Histories. Springer.*

If reproduction is very costly in terms of growth and survival, repeated (iteroparous) and/or delayed reproduction may evolve, provided that reproductive success at a later ages more than compensates for the loss of fitness incurred by not reproducing earlier. Otherwise a semelparous life history, in which all of the organism’s resources are allocated to a single reproductive effort, is optimal.

*Annual plants, including all grain crops and most domestic vegetables, are semelparous. Long-lived semelparous plants include century plant (agave), Lobelia teleki, and some species of bamboo.*


THE EVOLUTION OF THE RATE OF INCREASE

In general, the per capita rate of increase ($r$) of a genotype is the measure of its fitness, and it might be supposed that species would always evolve higher rates of increase.
Shorter life span, lower fecundity, and delayed maturation, all of which lower \( r \), can each be advantageous.

**Density-dependent factors** such as resource limitation or predation reduce birth rates or increase death rates.

The actual rate of increase of a population can be advantageous if it is lower than the intrinsic rate of increase (potential rate of increase).

"According to life-history theory, growth rates are subject to strong directional selection due to reproductive and survival advantages associated with large adult body size. Yet, growth is commonly observed to occur at rates lower than the maximum that is physiologically possible and intrinsic growth rates often vary among populations. This implies that slower growth is favoured under certain conditions. Realized growth rate is thus the result of a compromise between the costs and advantages of growing rapidly, and the optimal rate of growth is not equivalent to the fundamental maximum rate." Caitlin Dmitriew. **Biol. Rev. (2011), 86, pp. 97–116.**

"Moreover, even animals with unlimited access to food are often observed to grow at rates lower than their fundamental maximum. This implies that the optimal growth rate may in some circumstances be lower than the maximum possible, and that high growth rates are costly." Caitlin Dmitriew. **Biol. Rev. (2011), 86, pp. 97–116.**

As the population density approaches equilibrium (\( K \)), a more competitive genotype may sustain positive population growth while inferior competitors decline in density, have a negative \( r \).

- In some large mammal populations, competition does not affect the fecundity of the population until the population density reaches a number close to \( K \), the carrying capacity, and then fecundity is reduced and the birth rate declines with increasing density.

- In other large mammal population, the birth decline is linear with population growth and increase density.

Populations that are regulated by density-dependent factors and occupy relatively stable environments, predation or competition for resources often causes heavier mortality among juveniles than adults.

According to life-history theory, heavy predation on large, mature individuals should favor the evolution of greater offspring number.

If a juvenile reaches certain age, it has the probability of a long life. These conditions favor the evolution of iteroparous reproduction late in life, and long life span.

"Based on the evidence so far, the primary constraint on growth rate appears to be increased juvenile mortality due to predation." Caitlin Dmitriew. **Biol. Rev. (2011), 86, pp. 97–116.**

Under competitive conditions, juvenile survival can be enhanced by large size, so producing large eggs or offspring and fewer of them, may be advantageous.

Low intrinsic rate of increase – delayed maturation, production of few large offspring, long life span – are likely to evolve in species that occupy stable, competitive, or resource-poor environments.

In these populations, the rate of population growth is often close to zero because of density-dependent limitations.
Iteroparity is especially likely to evolve if juvenile mortality is high relative to adult mortality and if population density is stable.

An interesting observation:

**Cole’s Paradox and demographic models**

The models that have the strongest support from living systems are demographic. In Lamont Cole’s classic 1954 paper, he came to an interesting conclusion:

- For an annual species, the absolute gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size.

For example, imagine two species—an iteroparous species that has annual litters averaging three offspring each, and a semelparous species that has one litter of four, and then dies. These two species have the same rate of population growth, which suggests that even a tiny fecundity advantage of one additional offspring would favor the evolution of semelparity. This is known as Cole’s Paradox.

In his analysis, Cole assumed that there was no mortality of individuals of the iteroparous species, even seedlings. Twenty years later, Charnov and Schaffer showed that reasonable differences in adult and juvenile mortality yield much more reasonable costs of semelparity, essentially solving Cole’s paradox. An even more general demographic model was produced by Young.

These demographic models have been more successful than the other models when tested with real-world systems. It has been shown that semelparous species have higher expected adult mortality, making it more economical to put all reproductive effort into the first (and therefore final) reproductive episode.


