University College Maastricht

Course SCI2020

Genetics and Evolution

Academic year 2017-2018

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I. GENERAL INFORMATION

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Schedule

The Schedule will be provided by the office of student affairs.

2. INTRODUCTION

Ever since Darwin the theory of evolution has been the main unifying idea in life sciences. Molecular biologists study the structure and function of genes and proteins, anatomist study the structure of organs, physiologists study the mechanisms in our body, and ethologists study behavioral patterns displayed by animals (including man). Evolution connects all fields, since evolution tells us why these genes, proteins, anatomical structures, physiological mechanisms, and behavioral patterns evolved and came into being. If you are studying a structure (or mechanism), you may study that structure as an anatomist (or as a physiologist), but you can also study the structure as an evolutionist. Why did the structure evolve? How did it originate? The fact that an evolutionary analysis is always possible distinguishes life sciences from physical (and chemical) sciences. Why is evolution so important in life sciences? Why is evolution the cause of the main difference between life sciences and physical sciences? The answers to these questions are related to the problem what evolution is about.

Evolution is the modification of living organisms as the result of natural selection. Only living beings are subject to evolution. The reason is that natural selection is a force that operates on only *multiplying* organisms. Since organisms multiply, their numbers increase. If there were no selection forces, their numbers would increase indefinitely. However, organisms will die and some will die earlier than others. If there is genetic variation that affects their likelihood of surviving or reproducing, than organisms with characteristics most favorable for survival or reproduction will be selected. The result will be that these characteristics will become prevalent in a population. This is evolution in a nutshell.

The important point to notice is that natural selection cannot operate on entities that do no multiply. Take the example of a rock. We do not think that a rock is the product of natural selection. A rock does not multiply like a living being, and a rock does not have heredity: it cannot pass on a favorable characteristic to its offspring. Hence, there is no material for natural selection to act on in the case of the rock.

Evolution can only occur if there is genetic variation in a population. Hence for understanding the details of the evolutionary process, knowledge of genetics is indispensable. This is an important reason why both genetics and evolutionary theory are discussed in this course. The course will provide a basic grounding in those aspects of genetics, both population and molecular, that are needed to understand the mechanisms of evolutionary change. First, we will discuss transmission genetics. How are traits transmitted from one generation to the next. Understanding the laws of Mendel and how these laws explain qualitative and quantitative traits is of importance here. Genes code for characteristics, yet how do they code for a trait? This problem is studied by molecular geneticists: they have revealed that genes consist of DNA and that there is information encoded in this molecule. This information is replicated during cell division and transcribed and translated into proteins during the process of protein synthesis. Mutations, changing the genetic code, affect therefore the way proteins are constructed. In the first half of the course the task deal with general mechanisms such as the role of RNA in evolution, the organization of the genome, mobile genetic elements, regulation of transcription and maintenance of genomic integrity.

So natural selection can only operate on multiplying entities that are able to pass on favorable characteristics to the next generation. Since only organisms multiply, the theory of evolution is only applicable in life sciences. This difference between life sciences and physical sciences is so fundamental that it is translated into the formal distinction between two kinds of scientific explanations: *proximate* causal explanations and *ultimate* causal explanations. Proximate causal explanations deal with the physical and chemical causation of phenomena in life sciences. They say that there are all kinds of molecular processes that cause changes in organisms. *How* do physical or chemical forces cause these changes? The aim of proximate causal explanations is to identify causes of processes or mechanisms within the lifetime of a single organism. For instance geneticists elaborate the how during development individual characteristics evolve. Ultimate causal explanations try to explain *why* specific traits have been selected during the course of evolution. Why do many animals senesce, but many plants and fungi hardly at all? Why do most species have approximately equal numbers of males and females? These explanations tell us why specific genotypes have been preserved through selection on phenotypes. An evolutionary analysis is also about causation, but on a time scale of many generations and at the level of populations and species rather than individuals. In an evolutionary analysis one describes the causes as how natural selection shapes the traits or mechanisms under study.

3. COURSE OBJECTIVES

(1) Knowledge of genetics

- Knowledge of the essentials of Mendelian and quantitative genetics
- Knowledge of DNA replication
- Knowledge of protein synthesis
- Knowledge of genomic parasites and genome stability
- Knowledge of the essential of population genetics

(2) Knowledge of evolutionary theory

- Insight into the general characteristics of evolutionary theory
- Knowledge of the principles of kin selection, parental investment and game theory
- Insight into the evolution of aging
- Knowledge of sexual selection

- Knowledge of evolutionary transitions

(3) Insight into the use of evolutionary theory within biology, medicine and psychology
- The student can analyze a problem from an evolutionary perspective
- can report on an evolutionary analysis

4. STUDY MATERIALS

Essential reading:
We will use:
Stearns, S.C. & Hoekstra, R.F. (2005), *Evolution: An introduction*, Oxford University Press, Oxford, second edition.

Genetics:
Alberts, B. et al. (2008) *Molecular biology of the cell*. New York: Garland science, fifth edition.
Strachan, T. and Read, A. (2011) *Human molecular genetics*. New York: Garland science, fourth edition.
Alberts, B. et al. (2010) *Essential cell biology*. New York: Garland science, third edition.

Evolution:
Nettle, D. (2009) *Evolution and genetics for psychology*. Oxford: Oxford University Press.
Stearns, S.C. & Hoekstra, R.F. (2005), *Evolution: An introduction*, Oxford University Press, Oxford, second edition.

The following books are all available in the reading room or the study landscape:
Campbell, N.A. et al. (2008) *Biology*. San Francisco, Pearson, 8th edition.
Purves, W.K., Orians, G.H., Heller, H.C.,(2001) *Life; The science of biology*, Sinauer, 6th edition.
Barrett, L., Dunbar R. & Lycett, J. (2002), *Human evolutionary psychology*, Palgrave, NewYork.
Gilbert, S.F. en Epel, D. (2009) *Ecological developmental biology; Integrating epigenetics, medicine, and evolution*, Sinauer Associates Inc., Sunderland.
Gluckman, P., Beedle, A. & Hanson, M. (2009) *Principles of evolutionary medicine*, Oxford: Oxford University Press.
Nesse, R.M. & Williams, G.C., (1994) *Why we get sick*, Times books, New York.

Videos
The following videos can be used in connection with this block:
1. *Fetal attraction* [V2451]
2. *Nice guys finish first* [V1591]
3. *Chimps are humans too* [V3967]

5. ATTENDANCE AND ASSIGNMENT

The minimum *attendance* requirement for the tutorial group is 85%. There is no attendance requirement for the lectures.

Students who have not met the attendance requirement, but who have not missed more than 30% of the group meetings, will be given a provisional overall grade, but will not receive credits for the course until they have successfully completed an additional assignment. To qualify for an additional assignment a student may not have missed more than 30% of the group meetings and must submit a completed request form ‘additional assignment because of insufficient attendance’ to the Office of Student Affairs, within 10 working days after completion of the course.

The *assignment* consists of writing a paper during the course. The paper must handed in during the 7th week. You ought to write a report about (I) a topic related to genetics or about (II) a topic within the fields of evolutionary biology, medicine or psychology. The aim of this training is that you learn more about genetics and about evolutionary explanations and their application to phenomena.

Form of the assignment
The paper should be about 7-10 pages.

Evaluation of the assignment
The paper must be ready by the Friday of the seventh week. The mark you will obtain will be given to you by the tutor.

I Genetics

One way to study genetics is to study a specific topic. Below some topics are suggested, but you are allowed to choose a topic yourselves.

Some topics:

Evolution and the genetics of viruses
Evolution and DNA Repair
Evolution and mutations (chromosomal and/or point mutations)
Evolution and recombination
Evolution and genetics of mitochondria
Evolution and genomic imprinting
Evolution and quantitative genetics
Evolution and the genetics of the immune system

Another way to study genetics is to study a disease with a genetic cause. Through studying an (abnormal) disorder that is caused by a genetic mutation, you will get a clearer picture of the role of genes is the ‘normal’ development. The best way to start is to use internet sites. Two sites that deal with genetics and diseases are:

http://www.geneclinics.org
http://www.ncbi.nlm.nih.gov/

The second site allows you to enter OMIM (Online Mendelian Inheritance in Man). Both sites give you the opportunity to obtain information about the genetic background of several diseases.

Some diseases which can be linked to genetics and evolution are:

Rett syndrome
Autism
Obesitas
Anorexia nervosa
Prader-Willi syndrome
Angelman syndrome
Turner syndrome
Schizophrenia
Dyslexia
ADHD
Dementia
Williams syndrome

II. Evolutionary biology, medicine, and psychology

It is interesting to apply evolutionary theory to a specific topic and answer the question what an evolutionary approach adds to understanding the topic. Some topics are mentioned below, but you are free to choose a topic yourself.

List of topics

Morning sickness

Profet, M. (1992), Pregnancy sickness as adaptation: a deterrent to maternal ingestion of teratogens, in J.H. Barkow, L. Cosmides & J. Tooby (eds), *The adapted mind*, Oxford University Press, 327-365.
Forbes, S. (2002), 'Pregnancy sickness and embryo quality', *Trends in Ecology and Evolution*, 17, 115-120.
Flaxman S.M, Sherman P.W. (2008) Morning sickness: adaptive cause or nonadaptive consequence of embryo viability?, *The American Naturalist*, 172, 54-62.

Evolution of language

Hauser, M.D., Chomsky, N. & Fitch, W.T. (2002), The faculty of language: what is it, who has it, and how did it evolve?, *Science*, 298, 1569-1579.
Pinker S. & Jackendoff, R. (2005), The faculty of language: what's special about it? (2005), *Cognition*, 95(2), 201-36.

Evolution of warfare

Wrangham, R, (2006), Why apes and humans kill, in M. Jones & A.C. Fabian (eds.), *Conflict*, Cambridge University Press, Cambridge, 43-62.
Cunlife, B. (2006), The roots of warfare, in: M. Jones & A.C. Fabian (eds.), *Conflict*, Cambridge University Press, Cambridge, 63-81.
Buss, D.M. (ed.), *A handbook of human evolutionary psychology*, Wiley, New York, 2005.

Evolution of homosexuality

LeVay, S. & Hamer, D.H. (1994) Evidence for a biological influence in male homosexuality, *Scientific American*, may, 20-25.

Camperio-Ciani, A., Corna, F. & Capiluppi, C. (2004) Evidence for maternally inherited factors favouring male homosexuality and promoting female fecundity, *Proceedings of the Royal Society B*, 271, 2217-2221.

G.A. Schuiling, (2004), Death in Venice: the homosexuality enigma, *Journal of Psychosomatic Obstetery and Gynaecology*, 25, 67-76.

Intragenomic conflict and pregnancy

Haig, D. (1993), 'Genetic conflicts in human pregnancy', *The Quarterly review of biology*, 68, 495-532.

Virulence

Ewald, P.W., (1993), 'The evolution of virulence', *Scientific American*, April, 56-62.

Nesse, R.M. & Williams, G.C., (1994), *Why we get sick*, New York, chapter 4.

Lockhart, A.B., Thrall, P.H., & Antonovics, J. (1996), Sexually transmitted diseases in animals: ecological and evolutionary implications', *Biological Reviews*, 71, 415-419.

Ewald, P.W., (1994), *Evolution of infectious disease*, Oxford, chapter 3, 6 & 11.

Symmetry and partner choice

Gangestad, S.W. & Thornhill, R. (1997), 'The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry', *Evolution and human behavior*, 18, 69-88.

Mate choice and disease resistance

Potts, W.K. & Wakeland, E.K., (1993), 'Evolution of MHC genetic diversity: a tale of incest, pestilence and sexual preference', *Trends in Genetics*, 9, 408-412.

Wedekind, C. et al., (1995), 'MHC-dependent mate preferences in humans', *Proceedings of the Royal Society London B*, 260, 245-249.

Hill, A.V.S. (1999), 'Defense by diversity', *Nature*, 398,668-669.

Beauchamp G.K. & Yamazaki, K., (1997), 'HLA and mate selection in humans: commentary', *American Journal of Human Genetics*, 61, 494-496.

To resemble or not to resemble

Platek, S.M. et al (2002), 'Reactions to children's faces resemblance affects males more than females', *Evolution and human behavior*, 23, 159-166.

Christenfield, N. & Hill, E. (1995), Whose baby are you?, *Nature*, 378, 669.

Uniparental inheritance of mitochondria

Hoekstra, R.F. (2000), 'Evolutionary origin and consequences of uniparental mitochondrial inheritance', *Human Reproduction*, 15 (suppl 2.), 102-111.

Frank, S.A. & Hurst, L.D. (1996), 'Mitochondria and male disease', *Nature*, 383, 224.

Child Abuse

D.M. Buss, *Evolutionary psychology*, Allyn and Bacon, Boston, 1999, chapter 7.

Suggestions for the organization of your paper
Start the paper with a brief introduction to the topic that you are going to discuss. Explain why it is interesting to undertake an evolutionary analysis of the topic. Which aspects of the topic can be clarified with the help of evolutionary theory? Thereafter, in a separate section, explain what evolution is, what evolutionary explanations are (including the difference between ultimate causal and proximate causal explanations), and the evolutionary background and/or explanations relevant to your topic. Next, you should discuss the results of the empirical research relevant to your topic. What methods were used? What hypotheses were tested? And what were the results? Finally, you should discuss the specific problem raised in the introduction to your report. What answer(s) can be provided to the problem? What suggestions can you make on the basis of your results for future research?

Example
One example is the topic of “a fear of snakes” or a snake phobia. At first glance, this phobia appears to be a “deviation” rather than an evolutionary adaptation. In the introduction, this can be formulated as a specific problem. Is a fear for snakes a deviation or an adaptation? In addition, you can explain why it could be an adaptation. The different arguments for such a position can be presented. First, the fear has avoidance of snakes as a consequence and thus reduces the risk of deadly snake bites. In this sense, the fear actually increases the chances of survival. Second, empirical research shows that people develop phobias for only things that are dangerous (thus for snakes and not tea cups). This empirical data also points to adaptation. The proximate cause of the adaptation is certain environmental stimuli (“smooth and slippery animals”) that elicit the avoidance reaction; the ultimate cause of the adaptation is that people who develop a fear of certain animals have greater chances of survival than those who do not. The question for further research is why some people have a more or less simple fear of spiders or snakes while others develop a more excessive fear?

6. EVALUATION, EXAMINATION AND RESIT

The course will be concluded with a written examination on the subjects and literature relevant to the tasks and lectures. The exam consists of open-ended questions.

The total score you may obtain for this course is 10 points. A maximum of 7 points for the exam, and a maximum of 3 points for the paper.

The resit consists of doing a (new) written exam. In order to be eligible for a resit examination, you must have met the attendance requirement for the course and have done the assignment.

II. TASKS

Task 1: Evolution and medicine

Bram is surprised by the fact that Darwin’s theory of evolution is considered one of the most important scientific discoveries. The theory can, in his opinion, be summarized very simply: What is important in evolution is the survival of the genes. ‘What is so special about such a theory?’ is the question that Bram keeps asking himself.

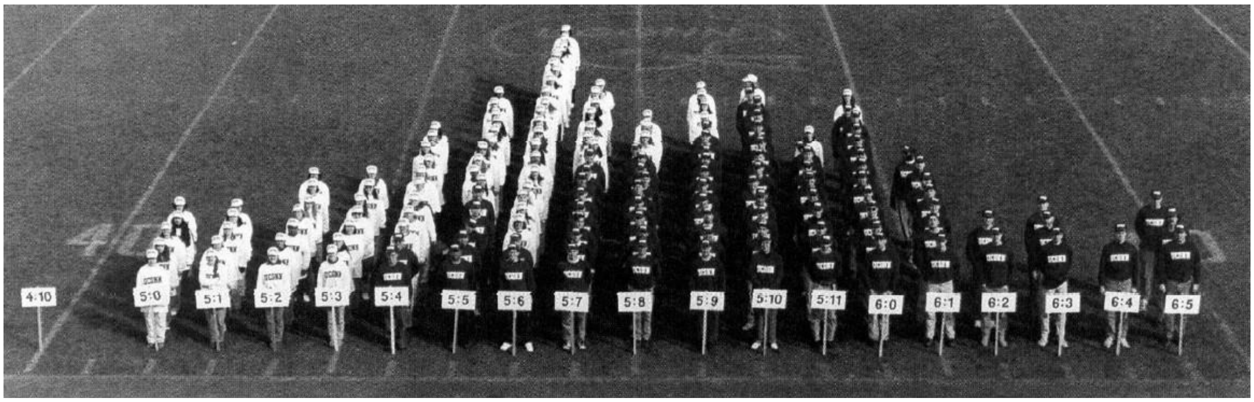
According to Remco, things are more complicated than this. Genes are important, but the selection of characteristics does according to him not occur at the genotypic level. For this reason, ultimate, evolutionary explanations also differ from the proximate explanations given in life sciences. But Remco wonders whether these evolutionary explanations are very useful. ‘Of what use are such explanations in actual practice? For example: for understanding diseases?’

In Hannah’s opinion, evolutionary explanations are relevant for understanding medical problems. ‘Take the example of symptoms of illness. Fever for instance suppresses a pathogen. Hence, this symptom has a function, since it protects against disease. Treatment of fever often increases the total duration of infectiousness. Illness should thus be studied as an adaptive phenomenon, no matter how crazy this sounds.’

Bram is still thinking about the role of genes. He remembers parts of an evolutionary story about sickle cell anemia, a disease that is caused by a recessive (autosomal) allele. The frequency of the allele that causes the disease is high in certain regions of the world. ‘If natural selection would be an important force in nature, then this allele should not occur’, says Bram.

Task 2: Mendel: rules and exceptions

2a.
Over the years, many scientists have looked into the patterns of inheritance. It quickly appeared that inheritance often did not follow Mendel's laws, but that simple Mendelian inheritance was more the exception than a rule. Many interesting traits are not distributed in populations in an all-or-nothing arrangement (for example pea color), but are quantitative, normally distributed features. An example of this is the distribution of height in the population (see below; women dressed in white, men dressed in black), but also many psychological traits follow a normal distribution. Can Mendel's laws be applied to explain psychological and other complex traits, or is a new set of laws required?



2b.
The fact that height is heritable is no surprise: if your parents are tall, you are likely to be tall as well. *Heritability estimates* of height vary quite a bit though: a study in Australia showed that height heritability was 80%, while a study in Western Africa reported only 65%. How do researchers get to these estimates? How can it be that they vary across studies? And most importantly: what does an estimate of heritability mean?

2c.
The laws of Mendel also apply to the sex chromosomes. Given that women have two X chromosomes (XX) while men have an X chromosome and a Y chromosome (XY), however, the pattern of inheritance for the genes on the sex chromosomes proceeds differently. The laws of Mendel predict that diseases linked to the X-chromosome will be more prevalent among men. Examples are hemophilia and color blindness. The frequency of such diseases is easy to calculate since the expression in males is mono-allelic.

Given these patterns of inheritance, it is hard to see why diseases located on the X-chromosome should be more prevalent in women than in men. However, there is an interesting exception to this rule: the syndrome of Rett (the frequency is about 1 in 15.000). This syndrome is a genetically caused disease that is far more prevalent among females (about 99% of the cases) than among males. The early symptoms of this disease are a disturbance in the (goal-directed) hand movements and the development of speech. During later stages autistic-like behavior is often observed. A curious fact to notice is the following: if men are bearer of the genetic disturbance, the symptoms are even more severe than in women.

There are also phenomena showing that the evolution of traits regulated by genes on the X-chromosome have been subject to different forces in males and females.

Exercises

(1) People of blood type A have a molecule called antigen A on the surfaces of their red blood cells. Blood type B corresponds to red blood cells with antigen B. A person with type AB has red blood cells with both the A and B antigens, and the red cells of a person with type O blood have neither antigen. The *I* gene encodes enzymes that place the A and B antigens on red blood cell surfaces. The three alleles are I^A, I^B, and *i*. People with blood type A may be either $I^A I^A$ or $I^A i$; type B corresponds to $I^B I^B$ or $I^B i$; type AB to $I^A I^B$; and type O to *ii*. Even though the I^A and I^B alleles are codominant, they segregate between generations.
Just as two different alleles at the same locus may interact in a heterozygote to produce a particular phenotype (like the AB blood type), also two genes at different loci may interact. The Bombay phenotype, for example, is a result of two interacting genes: the *I* and *H* genes. The relationship of these two genes affects the expression of the ABO blood type. The product of the *H* allele is an enzyme that inserts a sugar molecule onto a particular protein on the red blood cell surface. The recessive allele *h* produces an inactive form of this enzyme, that cannot insert the sugar. The *A* and *B* antigens attach to the sugar molecule that the *H* gene controls. As long as at least one *H* allele is present, the ABO genotype dictates the ABO blood type. However, in a person with genotype *hh*, the A and B antigens cannot adhere to the red blood cell, and they fall away. The person has blood type O, but may have any ABO genotype.

In a hospital two young women, Maria and Ineke, have delivered a baby on the same day. However, an unfortunate omission has been made in the identification of the babies, and now it is not clear anymore which baby belongs to which mother. Both Maria and Ineke have blood type A, Maria's husband Henk has blood type AB, while Jos, the husband of Ineke, has blood type O. Baby 1 has blood type A, baby 2 has blood type O. One of the doctors thinks that on the basis of these data the problem is solved. Another doctor suggests to also determine the Bombay genotype of the people involved. Baby 2 appears to have the *hh* genotype, while baby 1 is *Hh*. Maria and Henk are both *Hh*, Ineke is also *Hh*, while Jos has the *HH* genotype.

(2) John and Martha are contemplating having children, but john's brother has galactosemia (a rare autosomal recessive disease), and Martha's great-grandmother also had galactosemia. Martha has a sister who has three children, none of whom has galactosemia. What is the probability that John and Martha's first child will have galactosemia?

(3) Duchenne's muscular dystrophy is sex-linked (X-linked, recessive) and usually affects only males.
a. What is the probability that a woman whose brother has Duchenne's disease will have an affected child?
b. If your mother's brother (your uncle) had Duchenne's disease, what is the probability that you have received the allele?
c. If your father's brother had the disease, what is the probability that you have received the allele?

(4) A husband and wife are both heterozygous for a recessive gene for albinism. If they have dizygotic twins, what is the probability that both of the twins will have the same phenotype for pigmentation? Explain your answer.

(5) Consider the following dihybrid cross: AaBb x AaBb. If A and B are dominant, and a and b are recessive, how many genotypes are the result of the cross? What is the genotypic ratio underlying de 9:3:3:1 phenotypic ratio?

Task 3: The book of life

3a. The human genome has often been described as an instruction book describing a single large recipe 'how to design the organism', written in DNA code language (let's call it DNA*ish*). For a given person, her/his genes (more specifically, an individual's genotype) provide the cells a set of instructions of what the phenotype should look like.

The instruction book has some rules:

- The book consists of 23 chapters

- Each gene is a section in a chapter, consisting of paragraphs

- A section that describes a gene is interupted with paragraphs that do not relate to the recipe

- DNA*ish* uses only 4 letters (A, C, T, G)

- A word is formed by the combination of three letters

And some more rules…

- Every letter of the book has to be recoded in a second language first to understand the recipe.

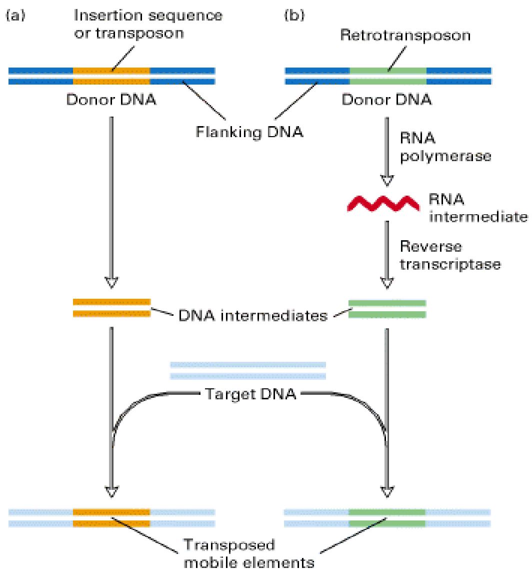
- The book can read itself, and make photocopies of itself.

- Photocopies are almost never perfect success, and sometimes some letters, words or paragraphs change in new editions.

Now, can you explain this metaphor?

3b. The human genome can be compared to a book. But the wealth of information a book contains is only available if it is read by someone. Likewise, DNA in cells waits to be read: it needs the activation of the protein synthesis machinery. Activation of the genome depends on environmental factors. For example, exposure to stress results in long-lasting behavioral changes, as studies of children who were born after the Dutch famine ('Hunger winter') have shown. Children born in this period were also more likely to develop obesity later in life. Interestingly, these environmental influences are mediated by so-called epigenetic processes.

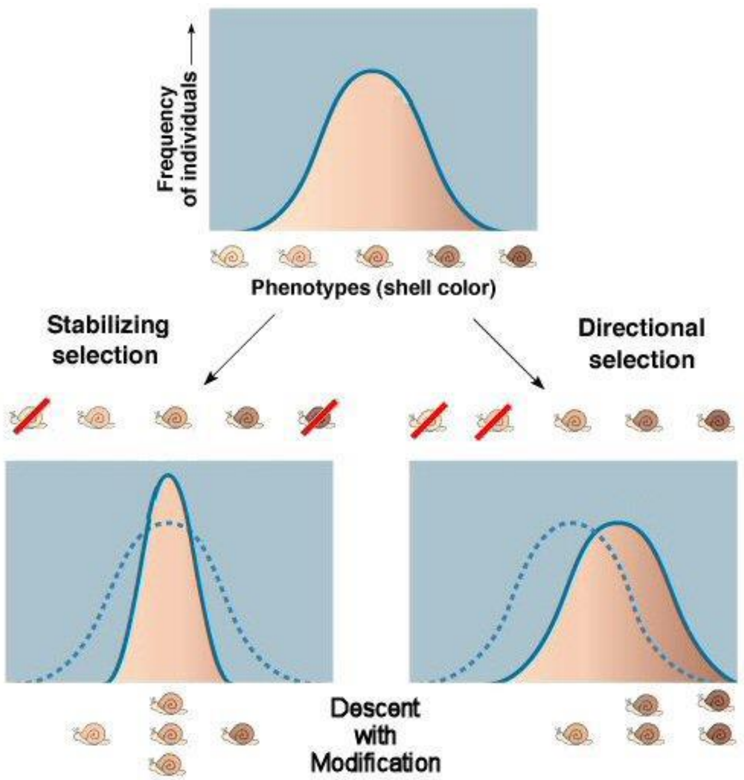
3c. The replication of retrotransposons and retroviruses like HIV seems to violate the central dogma. They have RNA*ish* as their language and use DNA*ish* of a host cell to make copies of this language. Since proteins are able to activate the transcription of genes, one may wonder whether this example violates the central dogma too.


(a)
Insertion sequence or transposon
(b)
Retrotransposon
Donor DNA
Donor DNA
Flanking DNA
RNA polymerase
RNA intermediate
Reverse transcriptase
DNA intermediates
Target DNA
Transposed mobile elements

Task 4: Population genetics: Adaptations and why some diseases are present at a high frequency

4a. If there is random mating in a population and if there is no selection, then the laws of Mendel tell us that the frequencies of the genotypes will remain the same over generations. However, Darwin taught us that there will be changes because there is selection resulting in adaptations. For understanding changes in the frequencies of genotypes, we have to compare the fitness-effects of alleles. Assume a simple model: there are only two alleles involved in the causation of the width of the hips of females, A and a. Suppose that allele a causes females to have wider hips than allele A. If wider hips enhance the fitness of females (for example because of less complications during the delivery), then it easy to see that selection will favor an increase of the frequency of allele a relative to allele A in the population. Yet it will take many generations before all females have the genotype aa, especially if a is recessive.

4b. Investigations of the *relative fitness* of genotypes revealed that populations can respond to selection in different ways. Two of such responses are shown in the figure below.



4c. Genetic diseases with severe effects that are due to a dominant mutation generally occur at very low frequencies in populations. Diseases due to recessive mutations occur at somewhat higher frequencies, but are still very rare. However, some severe recessive genetic diseases are conspicuously frequent, so that an additional explanation, next to mutation – selection equilibrium is required.

One example is Tay-Sachs disease which is strikingly common among descendants from East-European Jews (Ashkenazim): up to 11% of these people (many of whom nowadays are living in the USA) carry a copy of the mutation. Tay-Sachs disease is due to an enzyme deficiency and causes brain degeneration, paralysis, blindness, and death by age four.

Another example is CF, Cystic Fibrosis, another recessive disease. Early descriptions of CF mention the most seemingly benign of the symptoms – salty sweat. In fact, in 17th century England people had a saying: “Woe to the child which when kissed on the forehead tastes salty. He is bewitched and soon must die”. CF is characterized by defects in channels leading from certain glands, causing a variety of problems: extremely thick mucus and resulting infections in the lungs; a clogged pancreas and indeed salty sweat. As recently as 1960 a CF patient rarely lived past ten years of age. Today, better treatments may extend the lifetime to 30, sometimes 40 years. The frequency of the recessive mutation responsible for CF is in European populations remarkably high: about 1 in 50. This is another puzzle for geneticists.

Exercises

(1) In some populations, approximately 8% of the males have a particular type of color blindness (an X-linked recessive trait). What proportion of females would you expect to have this trait? What proportion of females would you expect to be carriers for this allele.

(2) A plant population has 289 individuals, some bearing red flowers, others white flowers. The red allele is dominant over the white allele. 246 plants have red flowers. Assuming the population is in Hardy-Weinberg equilibrium:
(a) What is the frequency of the white allele?
(b) How many of the red plants are expected to be heterozygous?

(3) Calculate the frequency of alleles A and B for the following three populations:

	AA	AB	BB
Population 1	20	40	40
Population 2	30	8	12
Population 3	72	122	91

What are the Hardy-Weinberg frequencies and expected genotypic numbers for the three populations? Are the observed frequencies of the genotypes different from the expected ones?

(4) The prevalence of autism is estimated to be 1 per 1000.
a. If a single dominant allele caused autism, what would the gene frequency of this allele be?
b. What would the frequency of the allele be if autism was caused by a recessive gene? What proportion of the population would be carriers if a recessive gene caused autism?
c. If autism is caused by two equally prevalent recessive alleles, what would be the frequency of each of those alleles? What is then the number of people carrying at least one risk allele?

(5) Suppose in a diploid, random-mating population two alleles occur at a locus A (A1 and A2). A1 is very common (frequency p=0.95). Due to recent environmental change A1 has become disadvantageous and is selected against. Consider two cases:

		A1A1	A1A2	A2A2
(a) A1 is recessive	fitness	1-s	1	1
(b) A1 is dominant	fitness	1-s	1-s	1

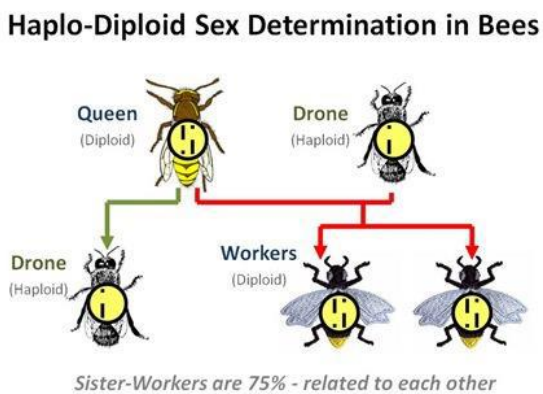
In which case will A1 reach a frequency of 0.5 faster? Why?

Task 5: Inclusive fitness theory and cooperation

The most important extension of Darwin's theory was developed by Hamilton and is called inclusive fitness theory. This extension is important for understanding social behaviour because Hamilton's theory is capable of explaining the evolution of cooperation.
Hamilton distinguished four types of social behaviour. These are defined as behaviours that have fitness effects (+ or positive effect; - or negative effect) on both the *actor* and *recipient* (see the table below).

	Effect on recipient	
Effect on actor	**+**	**-**
+	Mutual benefit	Selfish
-	Altruism	Spite

5a.
Selfishness and mutual benefit are abundant in nature. Spite rarely occurs (or is absent) for obvious reasons. Altruism occurs at a high frequency. However, altruism is not easy to understand in terms of Darwin's original theory because it is costly for the actor. Consider the example of sterile workers helping the queen in eusocial insects. This helping behaviour is an obvious example of altruism, but why was it selected?



5b.
Although Hamilton's theory predicts the evolution of cooperation, groups consisting of cooperators face the problem of free riders and cheaters. We can therefore predict that the evolution of cooperative behaviour required extra mechanisms e.g. suppressing free riders and cheaters. Since it is thought that especially humans are super-cooperators, most of these mechanisms occur only in human societies. Two interesting examples are summarized by the following sayings:

"I will scratch your back if you scratch mine'
'I will scratch your back if I am informed about you scratching the back of someone else'.

The first saying requires remembering a face, the second remembering a name.

5c.
A curious phenomenon, noticed by psychologists, is that humans are very sensitive to being observed by others. They are more likely to cooperate and to behave socially when they believe they are watched by others. Even the presence of pictures of eyes affects their behavior, as one study about the contributions to

a public good showed (see the figure 1 below).

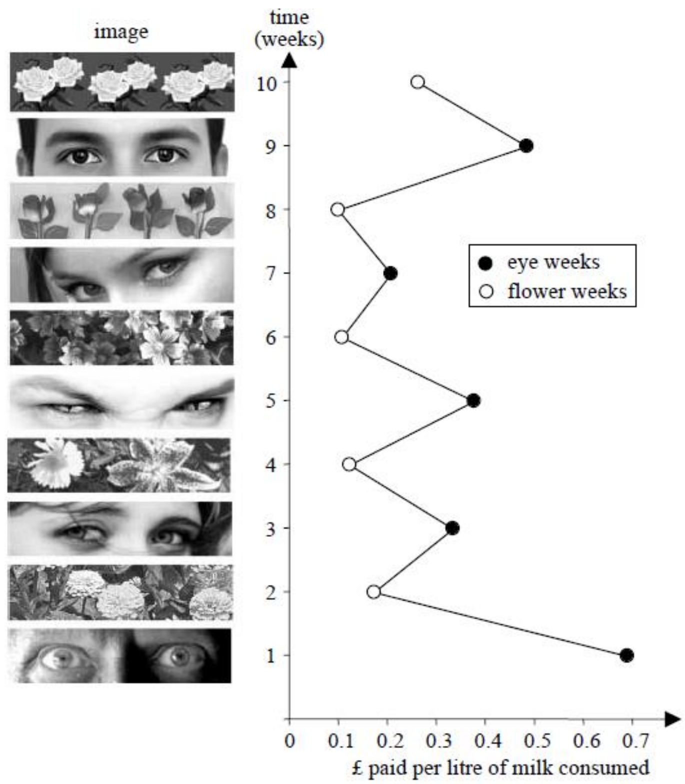


Figure 1. Pounds paid per litre of milk consumed as a function of week and image type.

Exercises:

1. What is the generic relatedness between a mother and her child, between two half-brothers, and between two brothers?
2. Haldane once said: ‘I would sacrifice my life for two brothers or eight cousins’. How can we understand his saying?
3. In haploid-diploid species (such as bees) males are haploid and females diploid. The reason is that females come from fertilized eggs and males from unfertilized eggs. What is, in this system, the genetic relatedness between two sisters, and between a sister and her brother (sister → brother)?

Task 6: Parent-offspring conflict and genomic imprinting

6a.

The most important extension of Darwin's theory, as we have seen, was developed by Hamilton's inclusive fitness theory. Trivers, following Hamilton's logic, argued that this theory explains conflicts between parents and offspring. For example Trivers argued that, because of fitness-advantages, mothers favour a shorter period of breast feeding, while children favour a longer period.

6b.

In cases of monogamy, fathers and mothers have the same interests in investing in offspring. In all other cases, the interests can be in conflict. The conflicting interests concern, among other things, the growth of offspring. This is not only the case for humans but also for mice. The latter can be seen from the following experiment.

> Of the two mouse species *Peromyscus polionotus* and *P. maniculatus*, the mice from the first species are monogamous and the mice from the second species are promiscuous. The body weights of individuals from the two species are the same. If a male of the promiscuous species is crossed with a female of the monogamous species, however, the body weights of the children are significantly higher. But if a female of the promiscuous species is crossed with a male of the monogamous species, the body weights of the children are significantly lower.

6c.

Genomic imprinting is the phenomenon that the expression of genes is dependent on the sex of the parent. Whether a gene was present in a male or female germ line in the previous generation can affect how the gene is expressed in the current generation. For example IGF2 (insulin growth factor 2) is only paternally expressed. Mice that inherit a disrupted paternal copy of Igf2 are born small. IGF2R (insulin growth factor 2 receptor) is only maternally expressed. This receptor functions as a 'sink' to internalize and degrade paternally produced Igf2 in lysosomes before the growth factor can execute its function. Mice that inherit a disrupted maternal copy of IGF2R are born large.

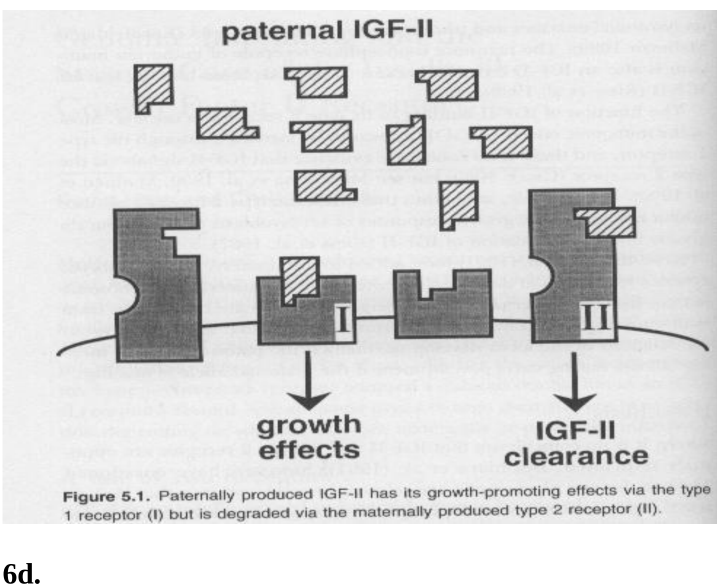


Figure 5.1. Paternally produced IGF-II has its growth-promoting effects via the type 1 receptor (I) but is degraded via the maternally produced type 2 receptor (II).

6d.

Hamilton's inclusive fitness theory is capable of explaining cooperation in terms of direct and indirect fitness benefits. However, the theory also predicts the evolution of free rides and cheaters. An example is the following. In species such as mice that huddle during the pre-weaning stage, heat production (as the result of burning brown fat) by one individual reduces the heating costs of other individuals. An individual's heat production is therefore beneficial for the other individuals in a litter. The heat produced may be seen as a collective good that increases inclusive fitness. Free riders are individuals that benefit from the heat produced by others but do not contribute to the common good. Interestingly, the paternal allele involved in heat production in offspring of mice is switched off, while the maternal allele is active.

Task 7: Evolutionary stable strategies

Game theory originated in mathematical theory and was later applied to the evolution of social behavior. Game-theoretic research on social behavior is concerned with frequency-dependent selection processes. How does the fitness of individuals displaying certain behaviors depend on what others in the population do? Examples of game-theoretic models are the Hawk-Dove model and the Prisoner's dilemma (see accompanying description). The Hawk-Dove model starts from the assumption that there are only two strategies in a population, namely Hawk and Dove, and the model is used to explain the evolution of threat behavior. The Prisoner's dilemma similarly assumes two basic strategies and is used to explain the evolution of cooperation.
In the following, a number of mathematical examples are presented for discussion in the study group.

Example 1: The Hawk-Dove model assumes two strategies. Hawk keeps fighting until the other gives up or he, himself, gets wounded; Dove threatens for some time or runs away when attacked. The pros and cons of the two strategies can be calculated when we assign numbers to them:
Cost of injury: -20
Cost of threat: -1
Profits: +30

Calculate the payoffs for four combinations of Hawk and Dove, and provide an answer to the question of which of the two strategies is an evolutionary stable strategy (ESS) in this case.

Example 2: Answer the same question using the following values:
Cost of injury: -30
Cost of threat: -1
Profits: +20

Example 3: The Hawk-Dove model assumes that individuals fight over a resource, such as territory. The model does not make a distinction between the owner of some territory and the intruder. We can also create a model in which a distinction is made between three strategies: Hawk, Dove, and Bourgeois. Bourgeois behaves as Hawk when he is the owner and as Dove when he is the intruder. Bourgeois can also play against Hawk, Dove, and another Bourgeois. When you start from the examples 1 and 2, can Bourgeois be an ESS then?

Example 4: Game theoreticians study behavior in terms of mathematical models. They also observe behavior once and awhile. In this context, game theoreticians are wildly enthusiastic about the observed cooperative behaviour that emerged between the Germans and the English during the First World War. For the cooperation was explicable in terms of the Prisoner's dilemma.

The prisoners dilemma game

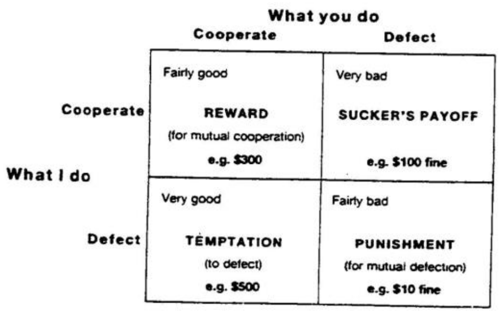


Figure: Diagram of the rewards that I can receive during this game

The game: Prisoner's dilemma assumes two players, you and me. Both have two possible choices, namely cooperate or defect (see diagram above). The choices must be made without the one knowing what the other chooses. Given these possibilities, there are four possible outcomes. The outcomes are rewarded as follows by the banker.

Outcome 1 We both choose to cooperate. The banker pays each of us $300.
Outcome 2 We both choose to defect. The banker fines each of us $10.
Outcome 3 I choose to defect; you choose to cooperate. The banker pays me $500 and fines you $100.
Outcome 4 You choose to defect; I choose to cooperate. The banker pays you $500 and fines me $100.

Which strategy should the players follow when playing this game? Imagine that you are playing the game. What would you do? You know in any case that the opponent can only follow one of two strategies. Let's examine the two strategies independent of each other. Imagine that your opponent chooses defection. It is logical that you, yourself, also choose defect. You will only get a fine of $10 and not that of $100. Imagine that your opponent chooses cooperation. What is your best choice? Once again, defect is the best choice. The conclusion is thus that defect is always the best strategy!
The point now is that both players can reason in the same manner. And this is where the dilemma arises. Given that both players realize that defect is always the best strategy, they also realize that they are both missing the relatively high reward of $300 they would receive if they should cooperate!

Task 8: Speciation

8a.

The title of Darwin's famous book is 'On the origin of species'. As indicated by the title, Darwin put forward the idea that species were not created by a Creator, but evolved. Starting from simple life forms, gradually more complex forms came into being. This process is often depicted as an evolutionary or phylogenetic tree.

The word species means literally 'kinds', but this fact hardly contributes to our understanding of what species are. Species are described on the basis of their appearances. Imagine how you should tell the difference between a Spider monkey and a Rhesus monkey. But such descriptions do not say much about speciation. How do different species originate? Is speciation fully understandable in terms of the microevolutionary processes we discussed earlier in this course, or are additional macroevolutionary processes necessary to understand the patterns observed in the fossil record?

Ernst is an evolutionary biologist who is interested in speciation. He studies two geographically isolated populations of warbles and notices that individuals of these populations only interbreed when they come into contact in a so-called hybrid zone. He wonders whether the two populations are two species.

8b.

Evolutionary genetics is haunted by the problem of race and racism. For obvious reasons: assigning people to categories with nearly inevitably associated value judgments about those categories has caused endless human anguish. Race typology is friable, too. Former strongly asserted racial groupings, such as Jews, Armenians, Italians, and the like, dissolve in the dynamics of human culture—even though geneticists can identify the differences between such ethnically identified populations and enable demographic history to be reconstructed.

Task 9: How did new individuals evolve?

9a.
The evolution of life has led to an increase in life's complexity. A number of evolutionary transitions occurred when life evolved from simple self-replicating molecules to multicellular organisms living in groups or societies. Two examples are (1) the transition from unicellular creatures to the symbiotic cell (the eukaryotic cell; recall that mitochondria, nowadays cell organelles of the eukaryotic cell, were originally free-living bacteria), and (2) the transition from symbiotic cells to the multicellular organism. These examples show that transitions may involve related or unrelated (lower-level) individuals. Hamilton's theory provides us with two theoretical principles with which we can explain transitions.

In the case of the eukaryotic cell, cooperation was beneficial because two different functions were combined in a new individual. In the case of the multicellular organism, there are no benefits related to combining different functions.
Genetic conflicts are limited in the multicellular organisms since the organism is derived from of a single fertilized egg cell. Since the genomes of the host cell and the mitochondria are unrelated, genetic conflicts, stemming from the behaviour of non-cooperative cells, are possible.

9b.
The emergence of multicellular organism resulted in a hierarchy of replicating units: individual organisms, cells and cell organelles. However, since all replicating units are undergoing adaptive evolution, genomic conflicts were possible. These selection forces are sometimes still visible. An example is a mitochondrial mutation known as 'petite' in yeast. Their colony size is small because of the mitochondrial mutation, but 'petite' mutations allow faster replication of the mitochondria. It is argued that uniparental inheritance of mitochondria prevents the evolution of selfish mitochondria.

Task 10: Sex and sexual selection

10a.

One of the explanations for the apparent evolutionary success of sexual reproduction has been called "the engine-and-gearbox model". Two non-functional cars, one of which has an irreversibly damaged engine and the other has a crashed gearbox, may yield a functioning car by using the gearbox from the first car and the engine from the second. The swapping of parts is analogous to the effect of genetic recombination, hence the name of this explanation. The broken engine may represent a serious mutation at locus A, while the crashed gearbox may represent a mutation at locus B. Recombination may create a genotype from which either mutation is missing. However, evolutionary biologists have serious doubts about the general validity of this explanation.

10b.

Sexual reproduction with meiosis and recombination arose 1.5-2.0 billion years ago. The first sexual organisms produced gametes of equal size, that were of two mating types. These two mating types did not differ in size. However, differentiation in size was the first step in the differentiation in sexes. Selection resulted in two types of gametes: large egg cells which were produced in small numbers; small sperm cells which were produced in large numbers. Now two key principles of sexual selection came into play. First, egg cells became expensive, sperm cells became cheap. Secondly, there arose different selection forces that put limits to the fitness of females and males. Given these two principles, the primary and secondary sexual characters evolved.

10c.

Given the differences between females and males mentioned above, different behavioral strategies can also be expected to manifest themselves in the sexual behavior of men and women. In the following, a number of differences with an evolutionary background are described.

In a relationship, there is often an age difference between males and females. The male is on average older than the female with whom he has a relationship.

A woman is always certain that the baby she is carrying is hers; a man can be deceived with regard to whether the baby is his or not. For this reason, men may be more sensitive to other aspects of infidelity than women.

Imagine that an unfamiliar but attractive man (or woman) approaches you and asks you if:
1) you'd like to have a cup of coffee,
2) you'd like to go home with him (or her), or
3) you'd like to go to bed with him (or her).

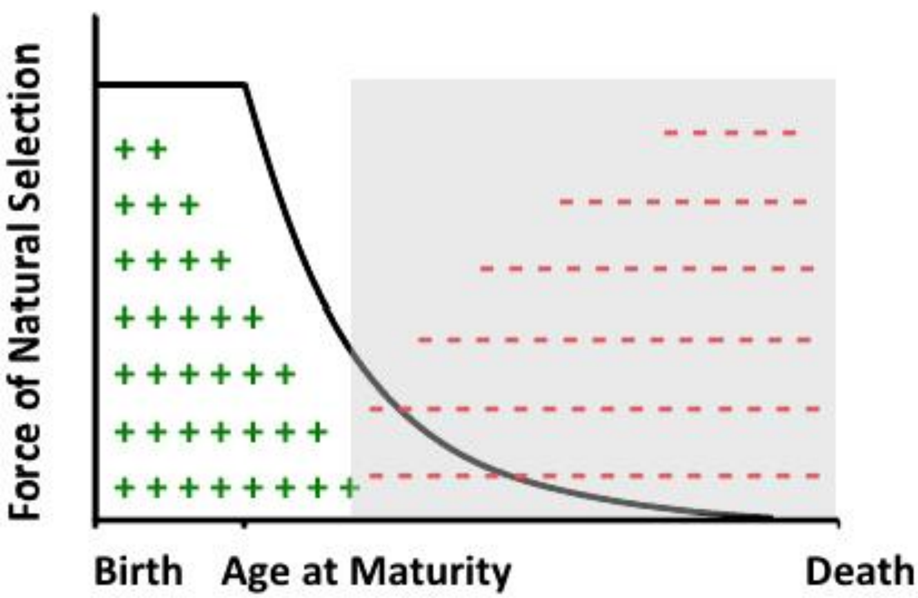
What do men and women do in these three cases?

Task 11: Aging and menopause

Aging is defined as “a decline in vitality and the functioning of organisms as a consequence of internal causes with increased chances of mortality as a result.” The usual explanation is that aging is unavoidable: it is a necessary and unstoppable process of wearing out. But just how strong is this argument? If organisms are equipped to go through an exceptionally complex developmental process, why should they not be able to accomplish the seemingly simple task of maintaining their bodies? If organisms were not to age, then they could reproduce forever. Animals nevertheless age, and the one species is earlier and faster than the other. For example, mice live to be a maximum of five years while bats (with a similar size and physiology) can live to be 35 years.

The existence of a phenomenon that points to an aging process but is not paired with increased mortality, namely menopause, is also rather strange. Apparently women who stop reproducing earlier than other women and thus use their energy in a different manner have been put at an evolutionary advantage.

Interestingly, menopause also occurs in killer wales. A recent study shows that, if there is no salmon abundance, post-reproductive females lead others to areas where there is some food.



LITERATURE

A = recommended reading list
B = additional and optional reading list

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APPENDIX: STUDY SKILLS AND PROBLEM-DIRECTED LEARNING

In the following, a summary of the different activities relevant to working in the study group is presented for review during the first meeting of the study group.

First meeting of the block

Does everyone know each other? Exchange of addresses and telephone numbers. Agree on the order for discussion leadership. The person leading the next discussion is responsible for taking notes on the present discussion. Make arrangements with the instructor for consultation of experts. Make arrangements regarding interim evaluations and agreements with contact people.

Working with the seven steps

Step 1: *Clarification of concepts*. In order to avoid misconceptions and misunderstandings, the concepts used in the task are clarified. In such a manner, a joint starting point for discussion is also established.

Step 2: *Problem formulation*. The core of the task is determined in order to further delineate the subject matter.

Step 3*. Problem analysis/brainstorming*. Refreshment and delimitation of the knowledge present in the group (activation of prior knowledge) and thereafter identification of as many explanations, alternatives, and hypotheses relevant to the problem as possible.

Step 4. *Problem analysis/systematic listing.* Ordering of explanations mentioned during brainstorming and establishment of any connections/relations thereafter.

Step 5. *Formulation of learning objectives*. Identify in light of the aforementioned explanations what knowledge is lacking and what issues remain unclear. On the basis of this information, formulate learning objectives.

Step 6. *Self-study*. Acquisition of new information in such a manner that you understand it and can apply it to the relevant learning objectives. In addition, critical reflection on already existing and new knowledge in order to make a link to the preliminary discussions and learning objectives. Such self-study also prepares one for efficient and effective participation in the study groups.

Step 7. *Reporting*. In discussion with one's fellow students, the answers to the learning objectives are sought and reported on along with any remaining questions or ambiguities. After completion of the final discussion, everyone should know for him/herself whether the new knowledge has been understood, the study materials have been examined in sufficient depth, and whether the new information can be adequately explained to others or not. Report using your own words and not directly from a book.

Leading a group discussion

Preparation. Preparation of an "agenda" provides for effective and efficient discussion. Ask each member what he or she has done and from which book(s). What you could not find should also be clarified.

Structuring. Ordering of different contributions, indication of the different lines of discussion, and monitoring of the relevance of the topics being discussed.

Summary. An outline with a number of the main points can help structure the meeting, be used to determine whether the material under discussion has been understood or not, and also be used to stimulate discussion by the group members.

Stimulation. Getting the meeting started and maintaining order. Posing specific questions helps structure the meeting, stimulate contributions, and promote in-depth consideration during the preliminary and final task discussions.

Reformulation. More precise formulation of what a fellow student has said in order to expand the understanding of the group and determine whether what was said by the group leader or another member of the group has been understood.

Conclusion. Statement of what has been done, what has been decided, and what has been agreed upon as the starting point for the next meeting.

Participation in the study group

Note-taking. Provision of an overview and clear depiction of the information exchanged during the study meetings by taking notes and drawing diagrams.

Provision of information. Actively telling fellow students what is known during preliminary discussions, reporting on what has been decided and deduced during concluding discussions, and supplementation or clarification of information provided by fellow students.

Information requests. Pose precise questions for explanation, clarification, or illustration of information from others and checking or expansion of one's own information.

Summarizing. Statement of the main points can help structure the meeting, stimulate discussion by group members, and aid determination of whether the material under discussion has been understood or not.

Active listening. Active evaluation of whether one's own (new) knowledge and that of one's fellow students is correct and contributes to a better understanding and better recall of the material. An active listening attitude stimulates both the group process and product.

Evaluation

Observation. Pay attention to the methods of working, processes, and norms at play in the group. This helps provide insight into the efficiency and efficacy of the meeting.

Analysis. On the basis of observations, the positive or negative influence of agreements that have been made (or not made), different procedures, and various behaviors on the course of the meeting should be determined.

Provision of feedback. Inform each other of any observations, irritations, or opinions in order to adjust the objectives of the group accordingly, produce better cooperation, and deepen the discussion.