Notes on Evolution and Population Genetics

Eth. & Behav. Ecol.
Biol. 287
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I. INTRODUCTION

A. Of all of the great generalizations in biology, the most important and central to understanding biology is the theory of evolution. Neither a full appreciation of organisms nor of their constituent parts and processes is possible without an understanding of evolutionary processes.

B. Before proceeding, we need a definition of evolution. The most accepted notion would be that EVOLUTION:

- is a change in morphological or behavioral characteristics (a **PHENOTYPIC CHANGE** that <u>reflects a genotypic change</u>)
- of a **POPULATION** (a group of organisms)
- over **GENERATIONAL TIME**.

Thus, it is distinguished from the **ONTOLOGICAL (DEVELOPMENTAL)** changes that occur over the life of an organism. An individual never evolves; instead, it undergoes developmental changes (including senescence and death).

However, the types and relative abundances of traits possessed by individuals within a population do change with time in ways that have nothing to do with the normal life span changes of an organism. These changes occur over generations and range from relatively small changes to the production of new, separate species. In all cases, the <u>PHENOTYPIC CHANGES ARE EVOLUTIONARY ONLY IF THEY RESULT IN CHANGES IN THE POPULATION'S FREQUENCIES OF VARIOUS ALLELES (ALTERNATIVE VERSIONS OF A GENE).</u> Another way of putting this is that for evolution to have occurred, changes must be ***HERITABLE***.

> **Note:** In this course we are concerned with behavioral phenotypic changes. I do not want to imply that changes in genotype with no easily discernible external changes are evolutionary -- they are. In the sense we will use it, a **PHENOTYPIC TRAIT** <u>is a morphological or behavioral attribute of an organism above the level of the gene</u>. Although modern molecular and population genetics has shown that differing alleles have different structures (since they have different nucleotide sequences) and further that allele frequencies (see below) might change without noticeable changes in behavior or large-scale structure. However, we simply are not interested in changes that ***<u>only</u>*** occur at the gene level in this course.

C. As you know, there have <u>historically</u> been two main ideas about whether or not organisms change in character over generational time.

1. At least since the start of the Christian era, the main view in the west has been one of **STASIS** or UNCHANGEABLE (IMMUTABLE) species. This is a direct outgrowth of literal interpretation of Judaic and Christian religious writings.

2. However, earlier many of the Greeks (and other cultures) believed in change, although they had no real observational basis for this believe.

3. **Evolutionary ideas** became intellectually fashionable in the west in the **late 1700**s, after the systematic work of **Linnaeus** revealed the bewildering number of animals and plants. (Linnaeus did not believe in evolution himself).

a. In particular, two early ideas about evolution and the origin of change came from:

i. The so-called **HYBRIDIZERS** who studied crosses between different forms or species of plants in hopes of understanding both genetics and the production of new forms:

ii. And from **LAMARCK** who late in the 1700s proposed an entirely different **mechanism of evolution**, **EVOLUTION VIA THE INHERITANCE OF ACQUIRED TRAITS**. In his system, what an organism did or learned in its life could be passed on to the offspring who would then possess the trait. Thus, the famous example of the evolution of giraffes' long necks due to their reaching for tree leaves -- their offspring were supposedly born with increasingly long necks. This is clearly an evolutionary theory, however, it is one that **relies on a mechanism that we know today to be incorrect**. However, Lamarck significantly helped pave the way for later workers.

b. Two mechanisms of evolution are presently supported -- **natural selection**, developed jointly by Charles Darwin and Alfred Russell Wallace in the late 1850s (and really developed principally by Darwin) and **genetic drift** developed largely by Sewall Wright in the 1920s and 30s.

D. Natural Selection and Genetic Drift are generally referred to as **THEORIES**.

1. It must be emphasized that theories in science represent ideas about reality that have been repeatedly tested and have withstood all tests of falsification. If you wish to read more about theory etc. in science consult any good introductory text.

2. The term theory does not refer to a relatively unsupported idea, as it does when used in everyday life. Instead, it comes much closer to the term "fact".

3. Moreover, EVOLUTION, as an idea separate from natural selection (which is a mechanism) is more on the order of **SCIENTIFIC LAW** -- it is something we know happens in many cases and we have generalized these cases into an **inductive generalization** that all populations of organisms evolve over time.

E. However, there is <u>**CONSIDERABLE DEBATE ABOUT THE MECHANISMS that result in evolution**</u> **but no debate among informed biologists about the reality of evolution.**

> **IMPORTANT NOTE:** I cannot emphasize too much that this entire discussion is a scientific one. <u>Questions of supernatural events involving the formation of species are outside the realm of science</u>. Science according to its very foundation assumptions cannot deal with such descriptions of universe -- it is outside of its purview. As scientists, we must keep this in mind. Thus when I say that the theory of evolution comes as close to fact as anything does, I am speaking in terms of using the usual standards and means of scientific investigation (see next class notes). I am not able to disprove events that by being given the name "SUPERNATURAL" imply that they are outside of normal physical laws.

II. MECHANISMS OF EVOLUTION

A. Mechanism is all-important -- Lamarck was correct that some sort of evolutionary process was responsible for the diversity that was observed, but his proposed mechanism was incorrect. At present, there are **two generally accepted mechanisms that produce evolution:**

- **NATURAL SELECTION**
- **GENETIC DRIFT AND RELATED FACTORS**.

Arguments among biologists about evolution tend to focus on the relative importance of these two.

B. Both of these mechanisms are **CONCERNED ONLY WITH HERITABLE TRAITS**. This means that there must be some genetic influence on the expression of the trait. Another way of putting this is that there must be some genetic basis for the particular trait. An important concept for heritable traits is that of allele frequencies. See the first appendix to learn more about alleles, allele frequencies, and evolution. (Learn that stuff).

C. Obviously, <u>the degree to which a trait appears to be influenced by heredity as versus the environment varies</u>. This is the source of the NATURE-NURTURE controversy in regards to behavioral traits. We will consider this in more detail in a couple of classes.

Two important points need to be made:

1. **ALL BIOLOGICAL TRAITS ARE INFLUENCED BY BOTH GENES AND ENVIRONMENT** (recall the earlier discussions about the way traits develop as an interaction between genetic and environmental interaction; also recall the discussions about heritability).

2. **SOME TRAITS AS COMPARED TO OTHERS APPEAR TO BE RESISTANT OR RELATIVELY INSENSITIVE TO ENVIRONMENTAL INFLUENCE -- THEY SEEM TO BE EXPRESSED THE SAME WAY IN MANY DIFFERENT ENVIRONMENTS.** We often speak of such traits as being heavily genetically influenced or **HIGHLY HERITABLE**. (We sometimes also say these

traits are **CANALIZED in their development** since they are relatively insensitive to the range of environments normally present). However, even with these traits, if the environmental change is great enough, their expression will change.

3. Nevertheless, <u>traits that are most HERITABLE for a given range of environments are most sensitive to evolutionary mechanisms</u>.

! We will look into the question of genes and environment later when we study behavioral genetics.
? Why are behavioral traits often not believed to be subject to evolution?

D. NATURAL SELECTION:

1. This was the mechanism announced jointly by **<u>Charles Darwin</u>** and **<u>Alfred Russell Wallace</u>** in **1859** (Darwin usually receives most of the credit since he devoted his entire life's work to idea and as a result provided the foundation for most research on evolution. Note once more that neither he nor Wallace should be given credit as the initiators of the idea of evolution -- what they did was propose the first workable mechanism for evolution (although not the only, see below)). They used the term **NATURAL SELECTION** to distinguish it from selective breeding practiced by plant and animal breeders; they referred to this process as **ARTIFICIAL SELECTION** (Many of their ideas about selection came from a knowledge of artificial processes -- they simply sought to extend these observations to naturally occurring processes.)

2. <u>Evolution by natural selection can also be referred to as</u> **<u>ADAPTATIONAL EVOLUTION</u>**. This means that it this type of evolution is characterized by the increase in traits in a population that enable their possessors to reproduce in a given environment. In fact, such traits themselves are often referred to as adaptations.

3. Darwin's and Wallace's postulates on the process of evolution by natural selection. It is more of a description of a process than a typical scientific hypothesis:

a. **<u>Variation exists in all natural populations.</u>** The fundamental fact of biology is variation and much of biology is an effort to explain variation. Due to their complexity, biological entities are never identical as compared to chemical species. (See **<u>Appendix 4</u>** with respect to the roles of Sex and Mutation).

b. **<u>To some degree this variation is heritable</u>**. (We will discuss this in great detail later in the behavioral genetics portion of the course; for the moment it is sufficient to state that large amounts of evidence suggest that many behavioral and morphological traits are influenced by genes.

c. **<u>Organisms possess the ability to reproduce at a rate high enough that there are not sufficient resources for the needs of all individuals</u>**. This was a basic insight supplied to Darwin by the work of the Scottish Economist Thomas Malthus who was very interested in resources and human populations.

! Review the **basics of population biology in Appendix 2** at the end of this set of notes.
? Note that economics and evolutionary biology are often closely linked intellectually. Why is this so? Is it dangerous as some (Lewontin and Gould) suggest? (And why do they make that suggestion?)

d. The result is that there will be times **when either resources are limited** or some other factor in the environment (such as the abundance of predators) **will potentially limit reproduction**. (See the section of Appendix 2 on logistic growth)

e. As a result of these factors, a **"struggle for existence"** (in the broad sense) **occurs**

i. In one sense it may be against other individuals in gaining environmental resources ("natural selection") or mates (sexual selection)

ii. Or it may be more indirect in terms of being better able to avoid predators ("natural selection") or simply against the elements

iii. Nevertheless, in all cases it can be said that **COMPETITION occurs** between different individuals. In this case the effects of the competition are seen simply in terms of the different rates of reproduction of different phenotypes.

? How might it be argued that competition is occurring when the primary selective factor is some aspect of weather?

f. As part of the competition, some individuals are more successful at reproducing.

g. As a result, **the next generation will tend to resemble those individuals who were the best "competitors" in the previous generation.** (Again, this is due to the heritable nature of the traits that conferred the competitive advantage).

1. Since the characteristics of the population have changed, this is evolution.

2. The mechanism for the change was Natural Selection

h. The behaviors and morphological characteristics that increase in the population as a result of natural selection are termed **ADAPTATIONS**.

i. Finally, Darwin and Wallace wanted to account not only for short-term changes in populations but also speciation. They realized that their mechanism, natural selection resulted in slow change, especially when compared to artificial selection. But the work of the great geologist Sir Charles Lyell showed that the earth was much older than people had previously realized and therefore that **there had been a lot of time available for these changes to occur.**

! Since the Darwin and Wallace evolutionary theory has been increased in power by its marriage to modern genetics and population biology. Of particular importance are attempts to measure differences in **fitness**.
Appendix 3 deals with the notions of what are called **direct, indirect and inclusive fitness.**
You only need to know about direct fitness for most of the course.
The concepts of indirect and inclusive fitness are dealt with during the final week or two and so best save them till then.

4. **Summary**: The central feature of the process of natural selection is the idea that certain phenotypic traits confer a **GREATER REPRODUCTIVE SUCCESS** on their possessors. This simply means they produce more offspring. An equivalent term **<u>INCREASED FECUNDITY</u>.** The result of this is that relatively more copies of these genes are present in the next generation and since they help to produce certain phenotypes, the associated phenotypes become more common.

a. Notice that we are dealing with a **RELATIVE ADVANTAGE** of one trait over competing traits (caused by competing alleles) in a population. **<u>See Appendix 3 for more about this</u>**.

b. Notice also that **the central idea is not SURVIVAL *per se***. A long life span means nothing if it is not accompanied by increased progeny.

1. <u>Usually, a longer life will correlate with greater fecundity</u> -- thus the phrase "survival of the fittest" [1]. Unfortunately, this type of selection, where life is longer than competitors, is often referred to as **NATURAL SELECTION**.

2. However, **<u>a trait may actually shorten the life span of its possessor, but if it nevertheless leads to increased reproduction over competing traits, it will increase in frequency</u>**. Often such traits are associated directly with attracting mates -- for instance making members of one sex very conspicuous and thereby increasing their chance of being killed by predators. <u>This particular type of natural selection is called</u> **<u>SEXUAL SELECTION</u>**. This topic is discussed in great detail in sociobiology and evolution courses.

E. GENETIC DRIFT

1. A **<u>second mechanism</u>** for evolution was proposed by largely by **Sewall <u>Wright</u>** in the 1930s (although it was foreshadowed by the earlier work of Hardy and Weinberg). This mechanism is called **<u>GENETIC DRIFT</u>**.

a. Genetic Drift is a form of evolution that does not usually result in Adaptation; it is usually said to be the evolution of **<u>NEUTRALLY</u>**

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[1] This phrase is traceable to neither Darwin nor Wallace -- instead it is from the writings of another great evolutionary thinker, <u>Spencer.</u>

ADAPTIVE TRAITS. Put another way, different alleles may increase or decrease with respect to each other but the change does not represent adaptation.

b. The **mechanism of genetic drift is CHANCE ASSOCIATED WITH RECOMBINATION IN SMALL POPULATIONS**

2. For genetic drift to work **the following factors must operate:**

a. The **alleles involved must not hold significant selective advantages over each other**

b. The **population involved must be quite small and sexually reproducing.**

c. There can be **no significant immigration or emigration of one allele as compared to others.**

For many populations and alleles, these factors hold true. For instance, many alternative alleles of genes produce proteins that are essentially equivalent in function -- the differences in their amino acid structure result in no noticeable difference in function in the environment the organism is found in.

Likewise, most local reproductive populations **(DEMES)** are quite small -- often less than 50 individuals (often much less). Finally, the migratory abilities of the individuals of many species are quite limited. Thus these assumptions are quite reasonable.

? The conditions mentioned above are all violations of a well know statement of the conditions for no evolution. What is the name of this famous statement?

3. **In the recombination process**, there are **two events that can easily affect the frequency of alleles in small populations:**

a. **Reductive division of meiosis**

b. **Syngamy**

? Explain why frequency can be affected by these two events.

4. As populations get smaller and smaller it becomes increasingly likely that alleles might change in their abundance in the offspring as compared to the parents. An analogy would be that in a small number of flips of a fair coin (here the probability of getting a head or tail is 0.5 -- these are analogous to two allele frequencies) one would expect that while roughly half of the flips would give heads and half tails, it would not be unexpected that if only 5 flips were made, all would be one type or the other. The more flips made, the closer the number of heads and tails would be to the expected 50:50 ratio.

Genetic drift works the same way -- one allele or the other increases simply at chance in small populations.

? Why is this evolution?
Why would it not work if the selective advantage of one allele over another were great?
Why would it not work if there were significant immigration or emigration of one allele over another?
Explain why genetic drift is said to result in neutrally adaptive evolution.

F. Phenomena Which Share Some Characteristics with Genetic Drift That are Important in Evolution

1. A related phenomenon is the **FOUNDER EFFECT** of Ernst Mayr. Here the idea is that new populations that are founded by relatively few individuals will be biased by the small founding genotype. Differences between them and other populations may have little to do with adaptation and instead simply be the result of chance. **The founder effect is an excellent example of the potential role that history can have in evolutionary change (see next section).**

2. Biased Migrations where one genotype preferentially leaves a population might also in some cases by a factor.

III. Some General Notes About Evolution:

A. NATURAL SELECTION attempts to adapt for the future by using the only predictor available -- the past.

1. To the extent that the environments remain the same for the offspring as the successful parents, the traits that are selected for will continue to be adaptations.

2. Note that an environmental change refers to more than just the physical environment. The biological environment is at least as important and generally changes more rapidly than the physical-chemical environment.

3. Thus, what conspecifics are doing (their adaptations) and the actions of other species can easily result in a trait that has been adaptive as being no longer adaptive even though the physical environment has not changed. We will focus both on the biological and physical environments in this course.

? What happens if a new allele enters a population (via mutation or migration) that confers greater advantage even thought the "environment remains the same? What does the environment an individual finds itself in include?

B. As a corollary to the above, NATURAL SELECTION CANNOT SEE INTO THE FUTURE. There is nothing **TELEOLOGICAL** about natural selection -- the only thing it produces is organisms that are relatively well-adapted to previous environments**.** We will come back to the importance of relative adaptation later -- but the key thing to realize is that for some allele to succeed evolutionarily, all it needs to do is improve the survival of its possessor (its survival machine) over individuals with alternative alleles)

Sometimes an adaptation that has proved useful in a certain environment or a certain behavior becomes useful in a new unique way -- often when the environment changes or the animal invades a new environment. While I hate the term since it implies seeing into the future, we often call such fortuitous adaptations **pre-adaptations**. This term should not be taken to mean that an animal sees into the future and adapts itself to some future environment -- it instead means simply that an animal **fortuitously** possesses a structure or behavior that was used in one context in one environment and is suddenly found to be useful in a new way in a new environment.

? Many writers (for instance the Jesuit Biologist/Philosopher Teilhard de Chardin) speak of evolution as a process directed towards some final end.
Can natural selection operate this way? What would be required?
Can the idea that all of evolution by natural selection has been directed towards the evolution of higher states of consciousness (ex.: de Chardin) be supported scientifically?
Is there progress in evolution?
Are trees of life ("lower and higher" forms on lower and higher branches) representative of progress or something else?
How would a biologist define the following terms?
Primitive, advanced, higher, lower
Can organisms be perfectly adapted for all times? For all times in a given environment?

E. HISTORY AND EVOLUTION: PHYLOGENETIC INERTIA AND TINKERING VS ENGINEERING:

1. Finally, keep in mind that every organism carries with it an evolutionary history. The way it looks is a consequence of:

a. Selection events that resulted in adaptations to features of previous environments

b. Many random events such as mutations, founder and drift events, and other chance events in the environment that occurred at crucial times affect the trajectory of the evolution of a certain line.

2. An organism must take the structures and behaviors that it already has and adapt these to meet the environment. Thus, it is often said that evolution proceeds by **tinkering** (small incremental changes of already existing structures and behaviors) and not by **engineering or design** (the *de novo* production of structures or behaviors for some specific purpose -- engineers use the best possible design for some function and are less the result of a compromise due to the necessity of working with pre-existing structures).

3. The results of this history are carried throughout the organism's genetic program. It is this program on which all alterations must be written and with which alterations must be at harmony.

a. An interesting phenomenon to be aware of is the fact that during evolution, the expression of certain genes is often either modified or blocked entirely, even though the genes continue to be part of the genome they become largely silent (this can easily be achieved through the action of regulatory genes that block or modify transcription).

b. We often see some of the evolutionary history when at later times these genes again become expressed as a result of some mutation -- in some cases it is simply a unusual expression and the archaic trait is referred to as an **ATAVISM or ATAVISTIC TRAIT** while on other occasions the old trait becomes useful, perhaps in a new context and we rapidly see its expression spread through the population.

4. **PHYLOGENETIC Inertia**: this is the tendency for structures or behavioral features to be preserved within a certain evolutionary line even when there have been significant evolutionary divergences between species. As an example we will discuss later, most species of balloon flies, regardless of whether they are carnivores or insectivores continue to use a silken balloon in their courtship ritual -- historically the male flies wrapped a dead mosquito in silk and presented it to females prior to mating -- all species use some variation on this behavior, even the most recently evolved forms that are nectivorous (eat nectar). In these a balloon is still produced but there is nothing inside of it -- thus the animals seem to be locked into using the balloon as part of courtship even though the balloon no longer has any function as a nuptial gift! That's phylogenetic inertia!

? What fish structures did our hands and feet evolve from? What are the analogs in these structures to fingers and toes? Did they have five? Do most terrestrial vertebrates have five digits per limb? Can you think of any successful groups, both extinct and extant than had/have less than five digits?
Is four limbs the key to success in terrestrial systems for animals that walk? Why do most terrestrial vertebrates have four limbs? Why are there rather more in arthropods?
What does all of this illustrate about the role of history in biology?

<u>General Review Questions</u>:

1. Should Lamarck be ridiculed? Did he make a contribution to modern biology? Explain.

2. One group of evolutionary biologists whose work we will discuss in this course can be called **adaptationalists**. In many ways, their view will take center stage in our approach.
An example of an adaptationallist whom you have probably heard of prior to this course is **Dr. Richard Dawkins** of Cambridge Univ. (author of *The Blind Watchmaker* and *The Selfish Gene* both very good reads). **<u>Adaptationalists</u>** posit that all structures are adaptations. In its most extreme form, adaptationalism posits that present structures are the best solutions that an organism can achieve to a certain problem.
Argue against the last viewpoint. Is every structure likely to represent an adaptation? Is the design of every important structure probably only the result of a chain of adaptation?

3 What do you think are the relative roles of random and selected evolution in determining animal behavior and structure?

4. Why is it that the mutation rate and/or recombination rate cannot account for the variation we observe in natural populations?

5. Evolution can be viewed as a device for solving the problem of continuation in the face of change. There are several ways that humans attempt to deal with change -- all have the common feature that they attempt to produce something new or even to restore something old that will help to deal with the change. However, we generally attempt to solve problems by some sort of conscious design -- we imagine, based on some knowledge what the best solution of many possible ones is and then we see if it works. We typically do not try all of a large number of possible solutions.
(a) Does evolution work this way? Sometimes the term "brute force" is applied to mechanisms where many solutions are tried to a problem and best chosen. Is this how evolution works? Explain your answer.
(b) What are the relative merits and disadvantages to the conscious design vs. brute force methods of solving problems? -- Some computer programs have been designed whose purpose is to try many possible solutions to some problem and then looking at the outcome. Why are computer programmers using such an "evolutionary" approach? (beyond the fact that computers are good at this sort of thing as compared to thinking).

6. Discuss history in evolution.

7. What will be fate of a new allele that causes its possessor to help others at the cost of its own reproduction? If a population of such animals existed (for instance, those which lowered their reproduction so that food resources used by all members of the species were not over-exploited, what would happen if a mutant, "selfish" allele appeared that caused its possessor to exploit the resources at a higher rate than its neighbors?

8. Suppose that in one environment -- a "young" lake with little vegetation, most individuals of some fish species exhibit a certain type of mating system. In this case, we'll say that system is monogamy (females and males pair off and do not mate with other individuals). However, over several generations the lake these fish live in changes as a result of ecological succession -- greater numbers of plants come to live in the areas inhabited by the fish. Now the most common mating system is polygyny (one male mates with multiple females; many males do not succeed in mating).
Discuss whether or not you have reasonable proof that organic evolution with respect to the mating system has occurred. How would you demonstrate whether or not the population had evolved with respect to mating system?

9. Terms or names to be able to concisely define:
Allele
Ontological, ontogeny
Evolution
Population
Heritable Trait
Inheritance of Acquired Traits
Variability
Phenotype
Trait
Allele Frequency
Founder effect
Teleological
Neutrally-Adaptive
Adaptation
Carrying Capacity, K and intrinsic rate of increase, r_0 (see **Appendix 2**)
intrinsic rate of increase (see **Appendix 2**)
genetic drift
A. R. Wallace
S. Wright

Appendix 1 – Allele Frequencies and Evolution:

1. To the extent that the expression of a trait is heritable, it reflects the presence of certain **ALLELES**. (See an Introductory Biology text if you do not know what alleles are).

2. If evolution occurs, therefore, not only with the frequency of manifestation of the trait changes, but so will the underlying **ALLELE FREQUENCIES.**

a. For a given locus, the total number and types of alleles present represents that population's **gene pool** for that locus. **Note:** the term gene pool is also often used to describe all of the alleles at all the loci within a population.

b. The frequency of all the alleles at a given locus must sum to unity (since they make up all of the possibilities at that locus). Thus, if we assume that at some locus in some population that there are three alleles (with a maximum of two in one individual) and the frequencies of each are p, q, and r then:

A1.1. $p + q + r = 1.0$

or

A1.2. $\sum$ (frequencies of all alleles) = 1.0

c. Allele frequencies are the **RELATIVE FRACTIONAL ABUNDANCES of the different versions of a gene IN THE POPULATION.** Thus, the frequency of a particular allele is the number of copies of that allele in a population divided by the total number of all alleles at that locus in that population. For example, in a population of ten individuals where 3 have genotype AA, 2 Aa and 5 aa; the frequency of allele A, p, is:

A1.3. $$p = \frac{total\ copies\ of\ A}{total\ alleles\ at\ locus\ "A"}$$

$$p = \frac{(2 * \# AA + \# Aa)}{2 * total\ \ \# individuals} = \frac{((2 * 3) + 2)}{2 * 10} = 0.4$$

iv. Note the emphasis on the fact that they are RELATIVE ABUNDANCES – within a population evolution occurs if **ONE ALLELE INCREASES AT THE RELATIVE EXPENSE OF ANOTHER – THUS, THE FREQUENCY OF ONE TRAIT WILL INCREASE AT THE RELATIVE EXPENSE OF ANOTHER**.

d. Allele frequencies are often also referred to as GENE FREQUENCIES, however, this is somewhat misleading and we will try to always speak about allele and not gene frequencies.

? What is the difference between an allele and a gene?
Is an allele also a gene?

Why is allele frequency the preferred term – what do you think might be misleading about the term gene frequency?

HERE'S A LITTLE PRACTICE FOR ANYONE NOT SURE OF THE WAY ALLELE FREQUENCIES ARE CALCULATED:

At gene locus A there are two possible alleles, A^1 and A^2.

They show LACK OF DOMINANCE and are HIGHLY HERITABLE. Thus, there are three phenotypes ("traits") that reflect the genotypes A^1/A^1, A^1/A^2, and A^2/A^2.

These animals have four generations a year. At the start and end of your two-year study you observe the following numbers of individual with each trait in your study population:

phenotype (genotype)	# at start of study	# at end of study
A^1/A^1	25	7
A^1/A^2	10	20
A^2/A^2	40	14

What are the allele frequencies at the two times? Which allele is more evolutionarily successful – or is it neither since their absolute numbers are decreasing?

MATH ANS.: start freq.(A^1) = $\frac{(2 * 25 + 10)}{2 * (25 + 10 +14)} = \frac{60}{150} = 0.40$

start freq.(A^2) can be calculated in a similar manner or since there are only two alleles, then

start freq.(A^2) = 1 – start freq.(A^1) = 1.00 – 0.40 = 0.60

Finish freq.(A^1) = 0.41; finish freq.(A^2) = 0.59

You discuss the rest!

Appendix 2: Population Biology

This section will be important when we get to the behavioral ecology portion of the course, most specifically when we consider optimality theory and life history strategies. No need to consider it heavily until then.

Be sure to understand the difference between exponential and logistic growth; for the moment, do not get into the math. It is provided for completeness. Do know the terms that are asked for in the general questions several pages earlier in these notes.

It had long been known that organisms were capable of very high rates of reproduction. Here is a short overview of what is relevant in understanding basic population dynamics:

(i) the size of a population at some time (***N_t***) is a result of the processes of birth, death, immigration and emigration. If we are interested in the **rate of change of a population,** $\frac{dN}{dt}$**,** then we can state that:

A2.1. $\frac{\Delta N}{\Delta t} = B+I-D-E$

where ***B, D, I*** and ***E*** are the birth, death, immigration and emigration rates (individuals/time). If we chose to ignore emigration and immigration and concentrate on birth and death (in fact emigration and immigration rates are often very small compared to B and D), then:

A2.2. $\frac{dN}{dt} = B - D$

and further if we define rates B and D as:

A2.3. B = b * N with a similar equation for *D*

where ***b*** is the rate of change due to birth (births per individual per time), ***N*** is the number of individuals and therefore ***B*** is total births per time, then:

A2.4. $\frac{dN}{dt} = B - D = bN - dN = (b-d)N$

we now define ***(b-d)*** as the rate of change in the population per individual (number of individuals per time per individual) and we will name it ***r***. This is also referred to as the **rate of increase**. Thus:

A2.5. $\frac{dN}{dt} = rN$

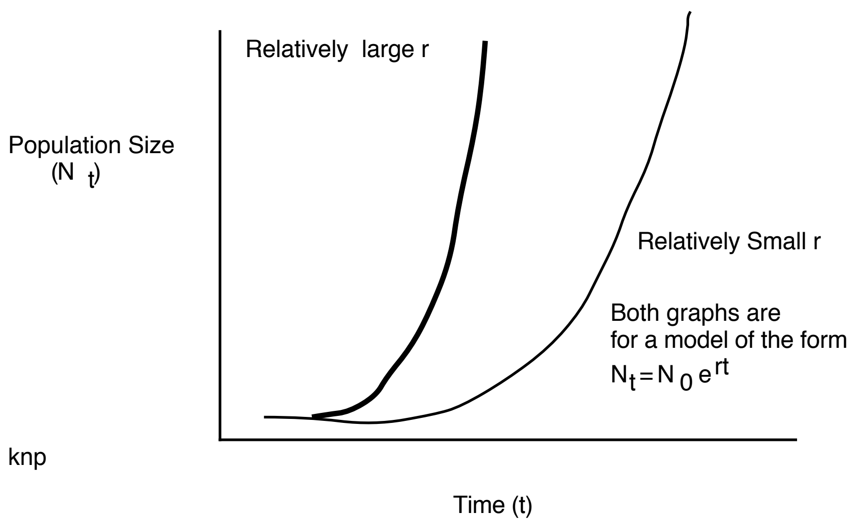
It is a simple matter to solve this equation (if you don't remember how or never learned, just trust me!):

A2.6. $N_t = N_0 e^{rt}$

where $\boldsymbol{N_t}$ is the population size at some time $\boldsymbol{t}$, $\boldsymbol{N_0}$ is the original (starting) population size, **e** is the base of the natural log system and $\boldsymbol{r}$ is the rate of increase.

Obviously this is an equation for exponential growth -- it accurately describes what any biological species will do when there are abundant resources and no other constraints. One thing to keep in mind is that different species do have different intrinsic growth rates, these are tied up with their particular ecological niche. Here is a graph of eq. #9 using two values for r:

Exponential Growth of A Population (no limits)



Darwin and Wallace also knew that this type of growth could not go on forever. They were aware of the work of the Scottish economist **Thomas Malthus** who had written a very important book on human population that argued that eventually a population, which grows exponentially, will outstrip its resources and growth will be brought into check by high rates of death or emigration and or lower rates of birth (less resources to devote to reproduction) or less immigration. When this happens we say that the population has reached its **CARRYING CAPACITY**, ***K*** (usually given as individuals). This is the point where one or more environmental features cause enough change in b, d, i, and/or e to cause the population to growth to stop and for the size of the population to remain roughly stable. We often say that the factors that cause the population to level off at *K* are **DENSITY-DEPENDENT**.

Mathematically, this idea is expressed as:

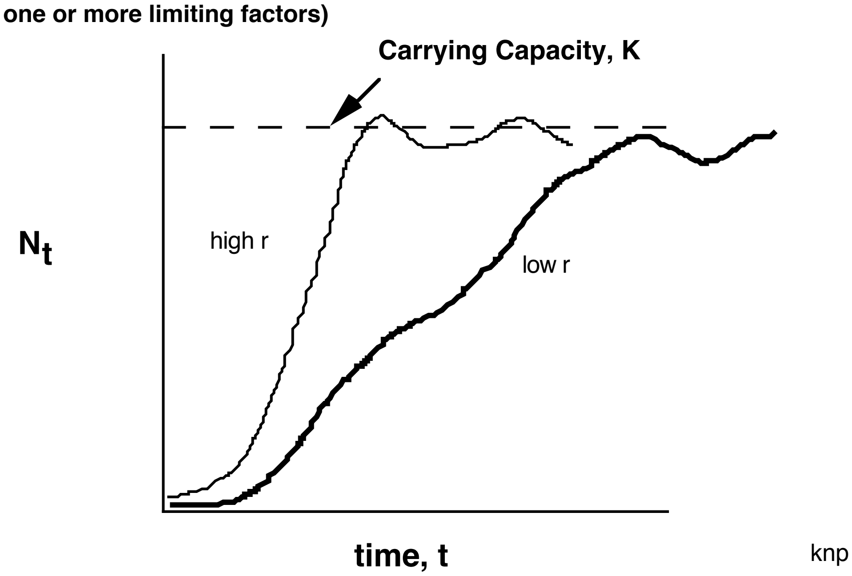
A2.7. $$\frac{dN}{dt} = r_o N \frac{(K-N)}{K} = r_o N \left(1 - \frac{N}{K}\right)$$

It should be obvious from either of these equations, that **as N approaches K, the rate of change $\frac{dN}{dt}$ will approach zero and if N exceeds K the population will decrease** (the rate $\frac{dN}{dt}$ becomes negative). If we solve the equation above so that we can plot it in a similar manner to the exponential growth equation, we get:

A2.8. $$N_t = \frac{K}{1 + \left(\frac{(K - N_0)}{N_0 \, e^{r\,t}} \right)}$$

<u>NOTE: This complicated expression is only given so that we can make a graph of population vs. time similar to the one just shown:</u>

Logistic Growth of a Population:
(where a population's growth is held in check by one or more limiting factors)



Incidentally, besides the density dependent factors we just mentioned, there are also environmental factors such as weather patterns (temperature, moisture, etc.) that affect populations independently of the population's size. Often these factors deal mainly with the physiological tolerances of the animal -- they are referred to as **DENSITY -INDEPENDENT** and have nothing to do with the carrying capacity. (For those of you who have had ecology , please excuse this very simplistic discussion of density factors!)

Appendix 3. Evolutionary Competition of Alleles or Organisms – The Concept of Fitness and its Measures

At the start of the course, it will be useful for you to understand the general notion of direct (Darwinian) fitness. We will consider the other aspects (inclusive and indirect) fitness during the final weeks of the course. You will learn how to calculate them at that time.

Note: You will not need to be able to calculate W_I yet; you just need to understand the concept and when another's offspring can be counted as another individual's W_I .

A. While the unit of evolution is the population, nevertheless, selection occurs between alternative phenotypes. Put another way, selection occurs between different individuals possessing different phenotypes.

B. There are a number of ways to measure the success of different individuals or alleles. All involve the **fitness concept.**

1. Simply put, fitness is a relative measure of the number of your genes (or if you are an allele, the relative number of identical copies of yourself) that are put into the next generation -- it is relative to what other individuals or alleles are doing. Thus fitness is always a **relative measure** although we will often use the shorthand "number of copies of genes in the next generation" keep in mind that what we are really talking about is the relative not absolute number of copies because evolution is based on relative changes of one type compared to another, not on overall population growth.

2. Fitness is always abbreviated by with a $\mathbf{W_{subscript}}$ where the subscript refers to the type of fitness that is being measured (see below) . Note that the name simply comes from Darwin and Wallace's idea that animals that best survived (i.e., were most fit) were most likely to leave a greater number of offspring. Thus it is a notion from the concept of natural selection. Nowadays we include sexual selection and while we still use the term fitness, what we are really referring to is simply **a measure of DIFFERENTIAL REPRODUCTION**.

C. **Measures of Fitness**

1. **DIRECT (Darwinian) FITNESS, (W_D)** :

(i) The relative number of grandchildren one has compared to others in the population. This measure is used to ensure that the individual's offspring are fertile. However, it is difficult to measure (you need to wait a long time); thus in situations where no inviabilty is suggested, it is more often that progeny are counted.

(ii) Progeny can either be individuals or in the case of an allele, the number of copies of the allele that are made.

(iii) Recall that fitness is always a relative measure, thus:

A3.1 $W_D = \frac{\text{(\# of offspring or copies produced by some individual or allele)}}{\text{(\# of offspring or copies of type producing the most)}}$

Thus, the most fit type will have W_D = 1.0; all others will either be less or equal to this.

? Part A: Calculate the fitnesses of the three genotypes for the locus "A":

genotype	average # of offspring/individual of that genotype
AA	2.0
Aa	2.7
aa	2.7

Part B: Try to make a calculation of the relative fitness of the two alleles A and a using the data above.

ans.: (part a: AA = 0.74, Aa = 1.0, aa = 1.0); (part B, A = 0.83, a = 1.0)

2. **INDIRECT FITNESS, W_i** : The relative number of progeny or offspring produced by close relatives <u>normalized by their coefficient of relatedness</u> or the number of <u>copies of alleles of identical descent</u> relative to competing alleles.

There are **<u>three important conditions</u>** that must be met for a reproduction to count as indirect fitness:

(i) The **<u>extra progeny (whether individuals or allele copies) must have been achieved by the relative as a result of some effort by the actor (reference individual</u>** -- the one whose indirect fitness is being calculated) that ***costs the donor in terms of its own direct fitness***. In other words, there must be a real sacrifice by the individual that will gain some indirect fitness units.

(ii) The donation must ***increase the reproduction of the recipient kin above what would have been possible without the "gift".***

(iii) As was mentioned above, the gain in W_I is not simply the relative number of extra offspring produced by near relatives; it must be normalized to the degree of relatedness -- thus an offspring produced by a half-sib will count only half as much as one produced by a full sib in determining indirect fitness.

3. Inclusive fitness (W_t): this takes into account the total reproduction that an individual has responsibility (or credit) for. Thus, it is the sum of both direct and indirect fitness:

A3.2 $$W_t = W_D + W_I$$

Inclusive fitness is difficult to measure since the indirect fitness component is especially hard to measure. Nevertheless, it is often the most useful measure of fitness especially when evaluating social behaviors.

APPENDIX 4: BRIEF NOTES ON THE SOURCES OF VARIATION: MUTATION AND SEX

An extremely important section!

A. Introduction: As we have learned earlier, evolution cannot occur in the absence of variation. It is important to understand something about the sources of variation:

B. The **ULTIMATE source of variation is MUTATION.** For most alleles under most conditions, you are probably aware that mutation rates are very low. Thus, the mutation rate of a typical eukaryotic allele (i.e., the NET frequency at which one allele turns into another) is roughly 0.00001 to 0.000001, meaning that of 100,000 to 1 million copies of a given allele, the net change into the competing allele would be about 1 allele changed!

? What is meant by net frequency when discussing mutation rates?

1. Obviously, if this were the only mechanism to induce changes in allele frequencies, then evolutionary rates would be extremely low. Other mechanisms must be involved and they will be discussed shortly.

2. The importance of mutation is simply to produce the raw material that causes variation; **evolutionary and reproductive mechanisms, not the mutation rate, are what will be responsible for the meaningful increase or decrease in frequency of a certain allele.**

3. The major source of the variation that selection can operate on is **RECOMBINATION**. In animals, recombination consists of the following mechanisms, all of which are related to sexual reproduction:

a. **MEIOTIC EVENTS:**

i. **Crossing-over** to produce new linkage groups of alleles on a given chromatid

ii. **REDUCTIVE DIVISION:** the production of haploid cells and in the process the re-shuffling of chromosomes inherited from the individual's parents

b. **SYNGAMY:** the fusion of the genomes of two different individuals

The key thing to realize here is that while recombination does not produce new alleles the way that mutation does, it does produce new combinations of genes that interact with the environment to produce unique phenotypes just as surely as a new mutant allele might. Recall that selection works on the organism's phenotype and that this phenotype is the result of extremely complex interactions between alleles and environment. As a result of recombination, every individual is different from every other (assuming no inbreeding!) even when constructed from a common gene pool.).