Lecture 5: Evolution, adaptation, natural selection, fitness.

Outline

Proximate vs ultimate causation
Terminology of evolution
4 evolutionary forces
- mutation
- drift
- isolation
- natural selection

Natural selection is the only force that produces adaptations
- Conditions for evolution by natural selection
  - variation
  - heritability
  - differential fitness
- Selection acts on phenotypes,
- Response to selection (evolution) occurs in genotypes
- Measuring heritability
- Adaptation vs abaptation: when the times they are a changin
- Tinkerer vs craftsman

There are two general approaches to explaining ecology and behavior.

Proximate explanations focus on *how* a phenomenon works (*what* controls the phenomenon, as it is now seen). How are sonar clicks produced by bats? How is their ear modified to perceive and use these signals? These are proximate questions.

Goal is to understand **mechanisms**. *How does trait work?*

Ultimate explanations focus on *why* a trait exists, rather than one of other plausible alternatives. Why do bats have sonar? Does it help them catch food, avoid predators, or both? These are ultimate questions.

Goal is to understand **evolution**. *Why does trait exist?*

Much of ecology uses the ultimate approach. To use that approach, must understand evolution.

Terminology

locus - location on chromosome making up a gene (plural = loci)
alleles - alternative forms of a gene that can occur at a given locus
gene - is sometimes used to mean locus, sometimes to mean allele)

genotype - the set of alleles carried by an individual (diploids: two alleles per locus)
phenotype - the physical trait produced by intrxn between genotype and environment
heritability (h^2) proportion of variation in phenotype that is due to variation in genotype.
adaptation - n. any characteristic (trait) that increases an individual's likelihood of survival and reproduction relative to individuals that lack the trait, or have an alternative form of the trait.
convergence - process of adaptation in which different ancestral stocks experience similar environments and thus become more similar (produces *analogous* traits, which have different origins but look similar)

(Fig. 1.12 Begon et al - convergence of placentals and marsupials)

adaptive radiation - process of adaptation in which populations from same ancestral stock experience different environments and thus diverge (produces *homologous* traits, which have same origin but look different)

(Fig. 1.9 Begon et al - Darwin's finches, *Geospiza*: oldest e.g. of adaptive radiation)

Evolution - change in allele frequency within a population. Note: when allele frequency goes to 0 or 1 it is **fixed**.

4 evolutionary forces

mutation - new allele arises by physical change in structure of DNA

genetic drift - random Δ in allele frequency by chance, important mainly in small populations (remember that variance ↑ as sample size (population size) ↓

isolation - 2 populations that exchange members (even just 1 disperser/generation) do not diverge genetically. Isolated populations can diverge due to drift or natural selection

(Fig 1.8 Begon et al: islands give good e.g. that rate of evolution ↑ as isolation ↑)

natural selection - the process of differential (survival and) reproduction of individuals

All 4 of the evolutionary forces (and less general ones such as meiotic drive) can cause change in allele frequency, i.e. evolution.

Only **natural selection** produces **adaptation.**

If three requirements are met, adaptive evolution by natural selection occurs:

1. VARIATION exists in phenotypic trait
2. variation is HERITABLE
3. variation produces DIFFERENTIAL FITNESS

genotypic level		phenotypic level
Genetic variability exists (alternative alleles exist)	→→→→	genotypic variation produces phenotypic variation (genetic variation is expressed)
		↓ ↓
phenotypic variation passes to offspring ($h^2 \neq 0$)	←←←←	some variations (survive and) reproduce more successfully (differential fitness) in given environment
↓ ↓ ↓		

distribution of allele frequencies will change through time (adaptive evolution)

Important to recognize:

1. *Selection and response*: Natural selection is the process of differential survival and reproduction by different individuals in a specific environment. *Selection acts on the phenotype*.

Response to selection is Δ in allele frequencies, if phenotypic variation is heritable, i.e. due to genetic variation. *Evolution occurs at level of genotype*. Evolution **IS** simply change in allele frequency.

2. Selection is caused by all aspects of the environment, biotic and abiotic. Therefore adaptation is relative to a given context. *An individual's fitness is relative to its environment.*

3. Whether an allele increases or decreases in frequency depends on what alternative alleles exist in the population. *Fitness is relative to alternative genotypes (phenotypes).*

4. *Heritability*: proportion of variation in phenotype that is due to genotype.

$$h^2 = \sigma^2_g/\sigma^2_p$$

Two identical genotypes, in different environments, may not produce identical phenotype. e.g. genetic contribution to height, but amount of food, especially when young, will also modify height.

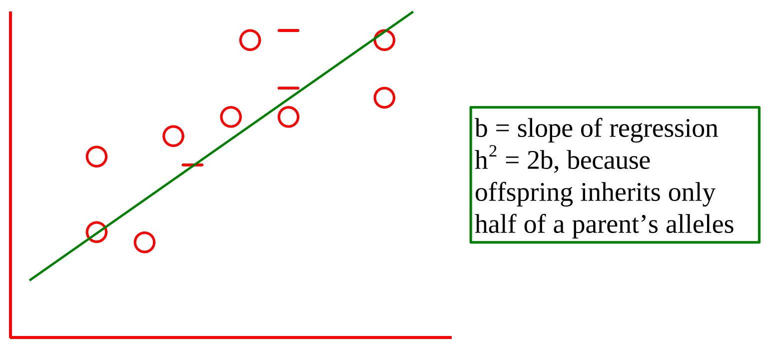
Two different genotypes, in the same environment, can produce similar or identical phenotype.

In other words, the phenotype is product of interaction between genotype and environment. Heritability measures what proportion of variation in the phenotype is due to the genotype.

There are many ways to estimate heritability. Most common is

Offspring-parent regression heritability:

Value of trait in offspring



Value of trait in father

(Fig. 3.12 Hartl)

Selection/response method to measure h^2 is less common, b/c it requires more data:

(Figure 3.4 Hartl)

a. Record mean values of trait for ALL adults from generation A: μ_A
b. Record mean value of trait only for adults that raise kids from generation A, i.r. hose that are 'selected for;: μ_s

c. The *selection differential*, S, measures the strength of selection

$$S = \mu_s - \mu_A$$

d. Record mean value of trait for all adults in next generation: μ_{A+1}

Typically, $\mu_{A+1} < \mu_s$.

Why? (1) Some parents had a 'good' phenotype (close to μ_s) but had a genotype other than the ideal one -- due to the environment and chance events, they expressed a good phenotype despite a poor genotype. (2) Gametes are passed on to next generation, so parental genotypes are never exactly duplicated in offspring (of sexually reproducing species). The mixing of alleles in meiosis, and mixing of alleles from mother and father, together ensure that traits are not passed on exactly.

e. The response to selection, R, measures how far the mean trait value has shifted after a generation of selection (of strength S)

$$R = \mu_{A+1} - \mu_A$$

f. Heritability measured as response/strength

$$h^2 = R/S$$

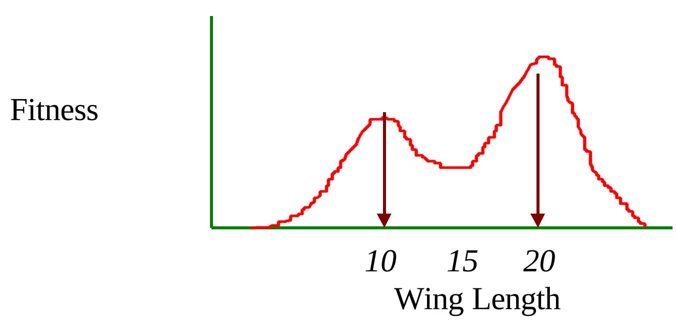
Some examples to show that there is evience that behavior is heritable to some extent

maze-bright and maze-dull rats:	$h^2 = 0.1$
drosophila courtship:	$h^2 = 0.6$
dispersal tendency in great tits	$h^2 = 0.3$

An interesting problem: traits under directional selection that have strong effects on fitness should have low heritabilities, b/c selection should rapidly eliminate alternative traits. Variation in direction of selection could keep heritability > 0.

***5.** *Adaptation* vs *abaptation.* Organisms have traits that have in past environments maximized fitness (abaptations). If habitat is now same as in evolutionary history, these traits will also maximize fitness in current environment (adaptations). But in rapidly changing environment, current traits might not maximize fitness.

6. Selection is a tinkerer, not a craftsman. Selection can only produce new solutions that are derived from current phenotypes.



Current mean = 10
Ideal length = 20
If mutations increase wing length in small increments, initial increase ↓ fitness, so wing length unlikely to evolve from local to global optimum

Types of Selection
Stabilizing, Directional, Disruptive
(Fig. 7.1 Pianka)