Introduction to Natural Selection

Natural selection is the fundamental mechanism of evolutionary change, operating through differential reproduction and survival of organisms with varying heritable traits. Darwin and Wallace independently recognized that individuals with traits providing better adaptation to their environment are more likely to survive and reproduce, passing beneficial alleles to their offspring. Over successive generations, advantageous traits increase in frequency while disadvantageous traits decrease, leading to adaptive evolution. The conditions for natural selection include:

(1) **variation** - genetic differences exist among population members,

(2) **heritability** - variations are heritable traits passed from parents to offspring. Then, natural selection act on this variation causing shift in the frequency of certain traits.

(3) **differential reproduction** – individuals (who survived) with favourable/advantageous traits produce more viable offspring than those with less favourable traits.

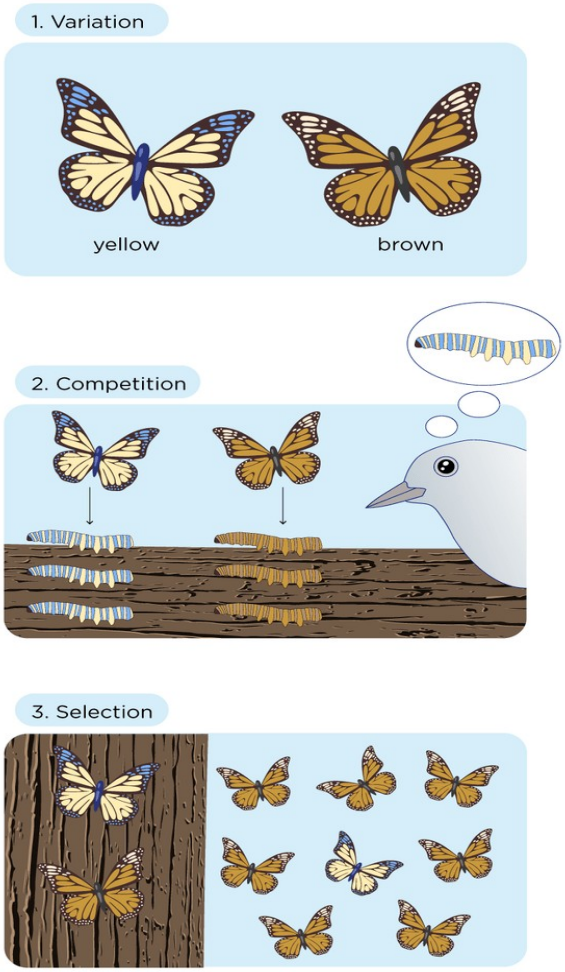
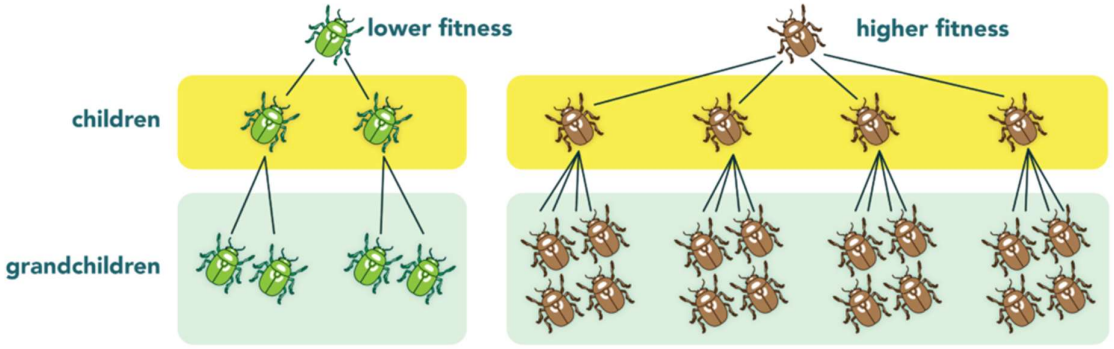


Fig: Simplified visual of Natural Selection at work.

1. Concept of Fitness

1.1 Definition and Types of Fitness



Fitness in evolutionary biology refers to an organism's reproductive success relative to other individuals in its population, not its physical health or athletic ability. It encompasses all components of survival and reproduction that contribute to passing genes to the next generation.

I. **Absolute Fitness (W_absolute)** represents the actual number of viable, fertile offspring an individual produces during its lifetime. For example, if a beetle produces 4 offspring during her reproductive years, her absolute fitness is 4.

II. **Relative Fitness (W)** expresses fitness as a proportion or ratio relative to other genotypes in the population. The most-fit genotype is assigned a value of 1.0, and all other genotypes are expressed relative to this standard. For instance, if genotype AA produces 100 offspring and genotype aa produces 80 offspring, the relative fitness values would be: W(AA) = 1.0 and W(aa) = 0.80. This allows comparison of fitness across different genotypes regardless of absolute population numbers.

1.2 Components of Fitness

Fitness comprises three measurable components:

I. **Viability (survival)**: The probability that an organism survives from conception to reproductive maturity. Organisms with traits that reduce predation risk or disease susceptibility have higher viability.

II. **Mating success**: The ability to locate and secure mating partners. Traits like physical attractiveness, elaborate courtship displays, or competitive abilities that increase mating opportunities enhance this component.

III. **Fecundity (fertility)**: The number of viable offspring an individual can produce. Factors affecting fecundity include parental investment, metabolic efficiency, and reproductive physiology.

The overall fitness of an individual is the product of these three components working together. A genotype might have excellent viability but poor fecundity, or vice versa, resulting in intermediate overall fitness.

2. Selection Coefficient and Mathematical Framework

2.1 Definition of Selection Coefficient

The **selection coefficient (s)** quantifies the intensity of natural selection against a particular genotype. It measures the relative reduction in the contribution that a genotype makes to the gene pool compared to the most-fit genotype in the population.

The mathematical relationship between selection coefficient and fitness is:

s = 1 - W

Where:

s = selection coefficient (ranges from 0 to 1)

W = relative fitness (ranges from 0 to 1)

2.2 Interpretation of Selection Coefficients

If s = 0: No selection against the genotype; it has equal fitness to the reference genotype

If s = 0.5: Selection removes 50% of the reproductive potential; the genotype produces only half as many offspring as the most-fit genotype

If s = 1.0: Complete selection against the genotype (lethal allele); the genotype produces no viable, fertile offspring

For example, if a genotype produces 65% viable offspring compared to the best-fit genotype:

Relative fitness (W) = 0.65

Selection coefficient (s) = 1 - 0.65

= 0.35 (representing 35% reduction in fitness)

2.3 Practical Example of Selection Coefficient Calculation

Consider a population of peppered moths where dark moths have higher survival rates due to industrial pollution:

Genotype	Survival Rate (Relative Fitness)	Selection Coefficient
Light (LL)	0.7	0.3
Heterozygote (Ll)	0.85	0.15
Dark (ll)	1.0 (reference)	0

The selection coefficient reveals that light moths experience 30% greater selection pressure than dark moths in industrialized environments.

3. Derivation of One Unit of Selection for a Dominant Allele

Step 1: Define Variables and Fitness

We consider a single gene (locus) with two alleles, **A** and **a**, in a large randomly mating population.

Alleles

A: Dominant allele (favoured by selection)

a: Recessive allele (selected against)

Allele frequencies

p: frequency of allele **A**

q: frequency of allele **a**

These must satisfy:

$$p + q = 1$$

Genotype frequencies before selection (Hardy–Weinberg)

AA: p^2

Aa: $2pq$

aa: q^2

Fitness (W)
Since **A** is dominant, the AA and Aa genotypes have the same highest fitness, which we set to 1 (this is a convenient scaling):

$$W_{AA} = 1$$

$$W_{Aa} = 1$$

The **aa** genotype is selected against; its fitness is reduced by selection coefficient s:

$$W_{aa} = 1 - s, \text{ where } 0 < s \leq 1$$

Step 2: Calculate Genotype Frequencies After Selection

To get the genotype frequencies **after** selection (before renormalizing to sum to 1), we multiply each initial frequency by its fitness.

Genotype	**Frequency Before Selection**	**Fitness (W)**	**Frequency After Selection (unnormalized)**
AA	p^2	1	$p^2 \times 1 = p^2$
Aa	$2pq$	1	2pq × 1 = 2pq
aa	q^2	1 - s	$q^2(1-s)$

Step 3: Mean Population Fitness ($\bar{W}$)

Mean fitness $\bar{W}$ is the sum of the unnormalized genotype frequencies after selection:

$$\bar{W} = p^2(1) + 2pq(1) + q^2(1 - s).$$

Simplifying the expression:

$$\bar{W} = p^2 + 2pq + q^2 - sq^2.$$

But:

$$p^2 + 2pq + q^2 = (p + q)^2$$

$$= 1^2$$

$$= 1,$$

Therefore,

$$\bar{W} = 1 - sq^2.$$

This $\bar{W}$ is used as a normalizing constant to ensure genotype frequencies sum to 1 again after selection.

Step 4: New Allele Frequency (p') After Selection

We now calculate the new frequency of the dominant allele **A**, denoted p', among the survivors.

The frequency of **A** is:

$$p' = \frac{\text{frequency of A alleles after selection}}{\text{total frequency of all alleles after selection}}$$

$$= \frac{\text{frequency of A alleles after selection}}{\bar{W}}.$$

'A' alleles contributed by each genotype

From **AA**: each AA has 2 copies of A, but since we are working with genotype frequencies (which already encode 2 alleles per individual implicitly), the contribution to allele frequency is just the genotype frequency after selection:
Contribution from AA = p^2.

From **Aa**: each Aa genotype carries 1 copy of A and 1 copy of a. So A gets **half** the heterozygote frequency:
Contribution from Aa = $\frac{1}{2} \times 2pq$

$$= pq.$$

There is no A allele in aa, so aa contributes 0 to A.

Thus, total frequency of A alleles after selection (unnormalized) is:

$$p^2 + pq.$$

Therefore, the new allele frequency p' is:

$$p' = \frac{p^2 + pq}{\bar{W}}.$$

Factor out p:

$$p' = \frac{p(p+q)}{\bar{W}}.$$

Using $p + q = 1$:

$$p' = \frac{p}{\bar{W}}$$

$$p' = \frac{p}{1 - sq^2}$$

This gives the updated dominant allele frequency after one round (one generation) of selection.

Step 5: Change in Allele Frequency (Δp)

The change in allele frequency, Δp, is the difference between the new and old frequencies of **A**:

$$\Delta p = p' - p.$$

Substitute $p' = \frac{p}{1-sq^2}$:

$$\Delta p = \frac{p}{1 - sq^2} - p.$$

Put everything over the common denominator $1 - sq^2$:

$$\Delta p = \frac{p}{1 - sq^2} - p \cdot \frac{1 - sq^2}{1 - sq^2}.$$

Therefore,

$$\Delta p = \frac{p - p(1 - sq^2)}{1 - sq^2}.$$

Simplifying the numerator:

$$\begin{aligned} \Delta p &= \frac{p - p + psq^2}{1 - sq^2} \\ &= \frac{psq^2}{1 - sq^2}. \end{aligned}$$

Thus, the change in frequency of the dominant allele **A** in one generation is:

$$\boxed{\Delta p = \frac{spq^2}{1 - sq^2}}.$$

Interpretation

The increase in frequency of the dominant allele (Δp) depends on:

- The selection coefficient s(strength of selection),
- The current frequency $p$of the dominant allele,
- The square of the recessive allele frequency q^2.

The term q^2 is crucial: when the recessive allele **a** becomes very rare (so q is very small), q^2becomes **extremely** small.

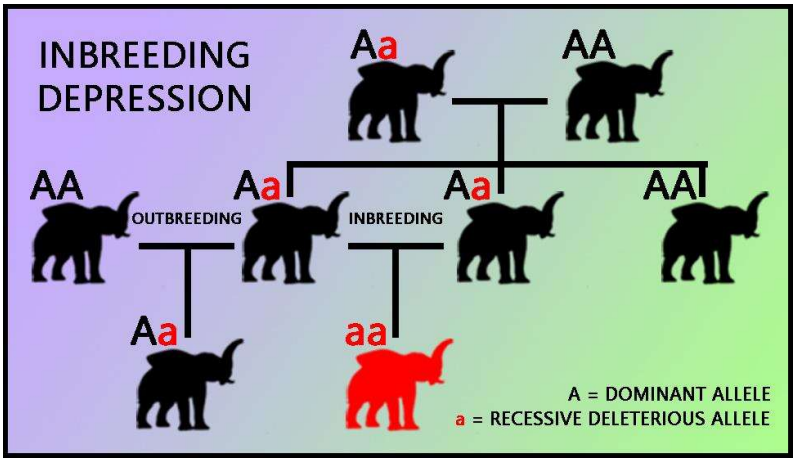
As $q \to 0$:

- $sq^2 \to 0$, therefore the denominator $1 - sq^2 \approx 1$,
- but the numerator $spq^2 \to 0$even faster.

This means Δp becomes tiny, and selection against **a** becomes very inefficient at low q. Biologically, that is because most remaining '**a'** alleles are hidden in **Aa** heterozygotes, which have the **same high fitness** as **AA**.

4. Genetic Load

4.1 Definition and Concept



Genetic load refers to the overall reduction in a population's average fitness caused by the presence of deleterious mutations or disadvantageous alleles. It represents the "cost" that a population bears due to the accumulation and maintenance of harmful genetic variants. Higher genetic load indicates more genetic disease burden and reduced population fitness.

4.2 Types of Genetic Load

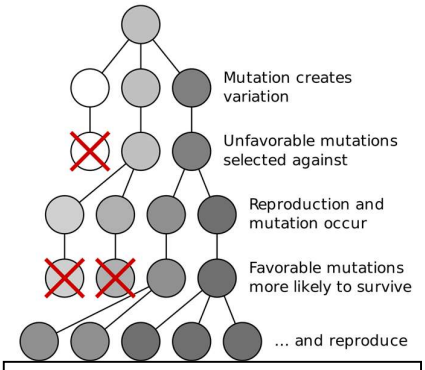


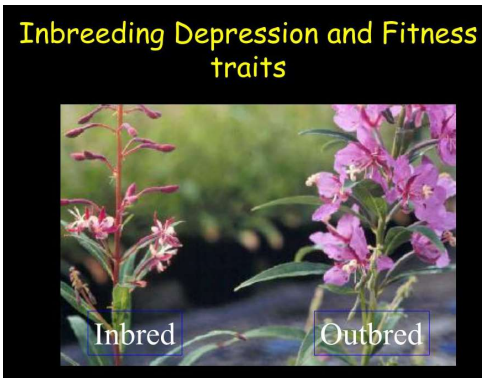
Fig: Disadvantageous mutated allele may accumulate (increase) across generation

I. **Mutational Load** arises from continuous input of deleterious mutations through mutation. Every individual carries some newly mutated, harmful alleles. In large populations, mutation-selection balance maintains these alleles at low frequencies. The mutational load depends on the mutation rate and the average fitness effect of mutations.

II. **Segregation Load** occurs in populations maintaining genetic variation through balancing selection *(Look at natural selection section: Balancing selection)*. When both alleles are maintained because heterozygotes have superior fitness (heterozygote advantage), homozygotes necessarily have reduced fitness, creating a load. This load is a cost of maintaining genetic diversity; for example, in sickle cell trait populations, both homozygotes (AA and SS) have reduced fitness compared to heterozygotes (AS).

III. **Substitution Load** (also called transitional load) arises when a population must replace an old allele with a new beneficial mutation. During the transition period, the population contains both alleles, and individuals carrying the old, less-beneficial allele have reduced fitness. This load decreases as the new allele approaches fixation.

IV. **Inbreeding Load** refers to fitness depression resulting from mating between close relatives. Inbreeding increases homozygosity, exposing recessive deleterious alleles and reducing heterozygote advantage, thereby increasing overall genetic load.



4.3 Significance of Genetic Load

I. **Conservation biology**: Small, isolated populations accumulate genetic load through inbreeding and drift, reducing population viability

II. **Agriculture**: Artificial selection can rapidly expose deleterious recessive alleles

III. **Human genetics**: Genetic load relates to disease incidence and population health management

IV. **Evolutionary theory**: Genetic load provides insights into the constraints and costs of evolution

5. Mechanism of Natural Selection

Natural selection operates through a non-random, mechanistic process:

Step 1: Heritable Variation
Populations contain genetic variation, with individuals differing in alleles at many loci. This variation must be heritable—differences must have genetic basis and be transmissible to offspring.

Step 2: Environmental Challenges
The environment presents challenges such as:

I. Limited food resources (competition)

II. Predation pressure

III. Disease and parasites

IV. Harsh climatic conditions

V. Competition for mates

Step 3: Differential Survival
Individuals with phenotypes better suited to their environment are more likely to survive these challenges. A moth's camouflage allows it to avoid predators; a plant's drought resistance allows survival in arid conditions. This differential survival is not random but predictable from phenotype-environment interactions.

Step 4: Reproductive Success
Survivors reproduce and transmit their genes to offspring. Importantly, not all survivors reproduce equally—some secure more mates, produce more offspring, or invest more parental care, leading to differential reproductive success.

Step 5: Allele Frequency Changes
Because advantageous alleles are more common in breeding individuals, their frequency increases in the next generation. Deleterious alleles decrease in frequency.

Step 6: Population Evolution
Over multiple generations, accumulation of frequency changes causes adaptive evolution—the population becomes better matched to its environment.

5.1 Key Principles

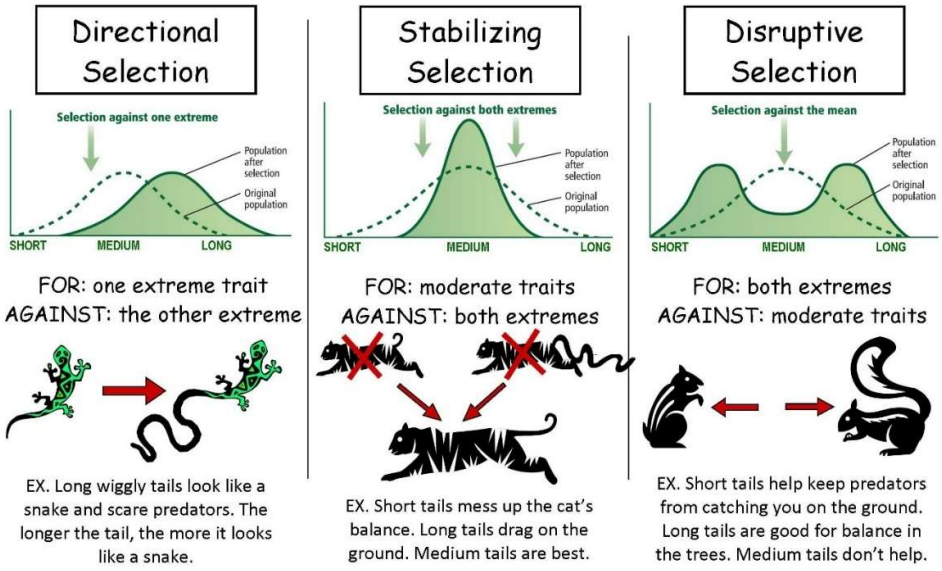
I. **The principle of differential reproduction**: Natural selection ultimately operates through differential reproduction (births), not just differential survival (deaths). An allele increasing survival but reducing fertility will decrease in frequency because fewer copies reach the next generation.

II. **Non-random mating and selection interact**: When females prefer certain male phenotypes (sexual selection), fitness differences arise from mating success, not just viability.

III. **Linkage and genetic architecture matter**: Linked genes affecting multiple traits (pleiotropy) can create complex selection scenarios where selection on one trait indirectly affects others.

IV. **Environment-dependence**: Fitness is environment-dependent. An allele advantageous in one environment may be deleterious in another, explaining variation in allele frequencies across geographic regions.

6. Types of Natural Selection



6.1 Stabilizing Selection

Definition: Stabilizing selection occurs when natural selection favours intermediate phenotypes while selecting against both extremes of the phenotypic distribution.

Effect on population:

I. Mean phenotype stays constant

II. Genetic variance decreases

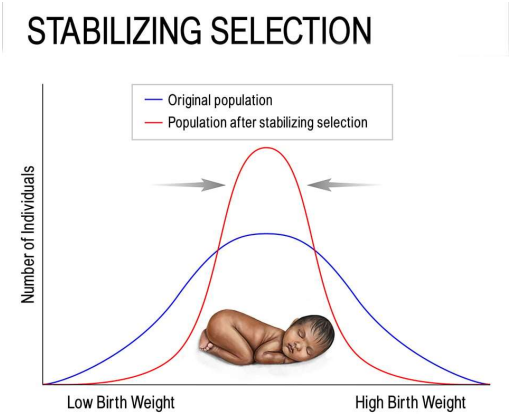
III. Population becomes more genetically homogeneous

IV. Phenotypic distribution becomes narrower and more peaked

Evolutionary outcome: Stabilizing selection maintains status quo and reduces genetic variation. It's common in stable environments where intermediate phenotypes are best-suited.

Example: Birth weight in humans

- Very low birth weight (< 2 kg) increases infant mortality due to developmental immaturity
- Very high birth weight (> 4 kg) increases obstetric complications and maternal/fetal mortality (death)
- Intermediate birth weight (~3.5 kg) has highest survival rates
- Natural selection consistently favours intermediate birth weights, maintaining this characteristic across generations



6.2 Directional Selection

Definition: Directional selection occurs when environmental changes or consistent selection pressures favour phenotypes at one extreme of the distribution, causing the population mean to shift toward that extreme.

Effect on population:

I. Population mean shifts in one direction

II. One extreme phenotype increases in frequency; opposite extreme decreases

III. Genetic variance may initially decrease (if selection is very strong) but can increase if standing variation exists

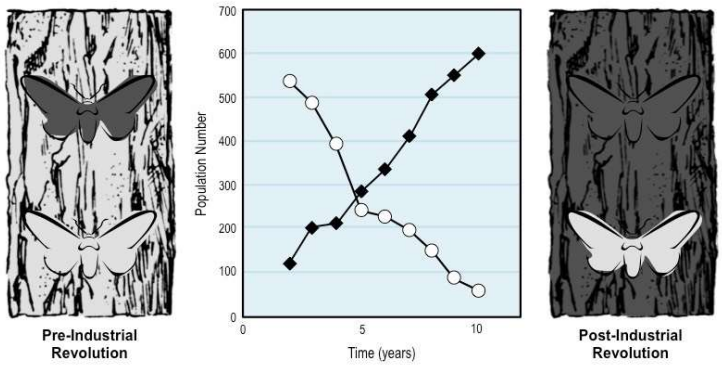
IV. Allele frequencies shift consistently in one direction

Evolutionary outcome: Directional selection drives adaptive evolution, causing rapid allele frequency changes and phenotypic evolution. It's particularly strong when environmental conditions change or new environments are colonized.

Example: Peppered moths in industrial England

I. Before Industrial Revolution: Peppered (speckled) moths were common; dark mutations were rare

II. Mechanism: Dark phenotypes were easily spotted on light lichen-covered tree bark by predatory birds



III. Environmental change: Coal-burning factories created dark soot; trees turned dark

IV. Selection reversal: Dark moths now had camouflage advantage; light moths became conspicuous

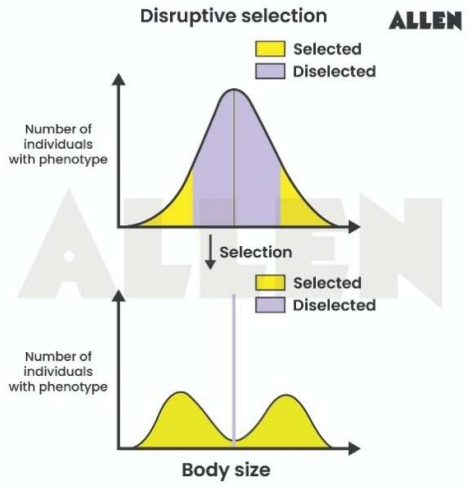
V. Result: Dark moths rapidly increased from <1% to >99% of population in industrial Manchester within 50 years

VI. Mechanism: Directional selection favouring dark coloration despite negative effects on viability (dark moths are more heat-absorbent)

VII. Modern reversal: After Clean Air Act (1956), air pollution decreased; light moths increased again

6.3 Disruptive Selection (Diversifying Selection)

Definition: Disruptive selection occurs when both extremes of a phenotypic distribution are favoured while intermediate phenotypes are selected against.



Effect on population:

I. Genetic variance increases

II. Population splits into two or more distinct phenotypic classes

III. Intermediate phenotypes are eliminated

IV. Bimodal or multimodal phenotypic distributions may develop

Evolutionary outcome: Disruptive selection can drive speciation by increasing population divergence and may lead to reproductive isolation.

Example: Oyster shell size

- Shallow water oysters: Light coloration camouflaged in sand (selected for)
- Deep water oysters: Dark coloration camouflaged in shadows (selected for)
- Intermediate water oysters: Medium coloration matches neither sand nor shadows (selected against)
- Result: Population evolves two shell-color phenotypes; intermediate phenotypes rare

****Balancing Selection****

Definition: Balancing selection maintains multiple alleles or phenotypes in a population at stable frequencies, preventing fixation of any single allele.

Major mechanisms:

I. **Heterozygote advantage**: Heterozygotes have higher fitness than both homozygotes

II. **Frequency-dependent selection**: Fitness depends on allele frequency; rare alleles have advantages

III. **Environmental heterogeneity**: Different environments favour different phenotypes

IV. **Sexual selection**: Females prefer rare male phenotypes

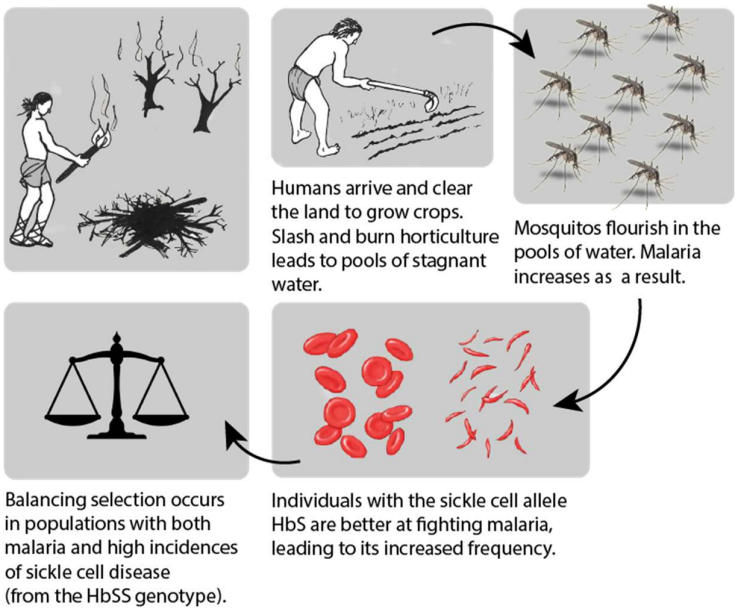


Figure Explanation: In a typical population, individuals with normal RBCs are more frequent. However, in regions where malaria is highly prevalent (such as parts of Africa), individuals with sickle cell trait have a survival advantage because sickle cells confer resistance to malaria. This creates a balancing selection effect where the frequencies of individuals with normal RBCs and those with sickle cell trait reach an equilibrium, maintaining both alleles in the population at relatively stable levels.

Effect on population:

I. Genetic variation maintained at constant frequencies (balanced polymorphism)

II. Population reaches stable equilibrium

III. Multiple alleles coexist indefinitely

7. Density-Dependent Selection

7.1 Definition and Concept

Density-dependent selection occurs when the fitness of different genotypes varies depending on population density (number of individuals per unit area). Unlike traditional models assuming constant relative fitness, density-dependent selection recognizes that fitness differences between genotypes change as populations grow or shrink.

7.2 Mechanisms of Density Dependence

Competition for limiting resources: At high population densities, individuals compete intensely for food, water, nesting sites, or light. Genotypes with different competitive abilities have fitness values that depend on density.

I. At low densities: All genotypes have abundant resources; fitness differences minimal

II. At high densities: Genotypes with superior competitive ability have higher fitness relative to less-competitive genotypes

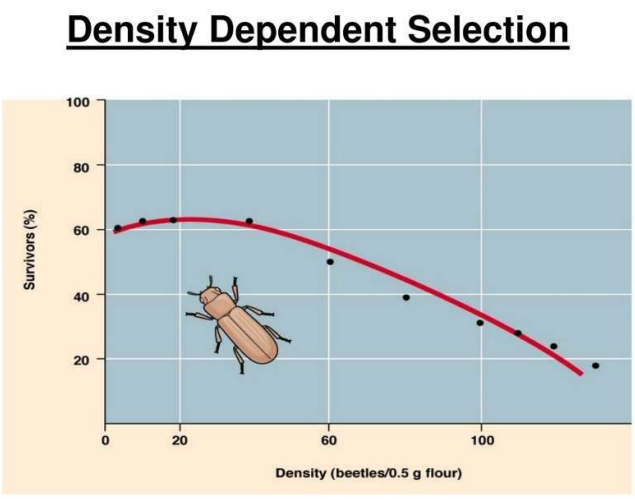


Fig Explanation:

Low Density (Population) = More resource = More Survival

High Density (Population) = Compete for resource = Less survival

Disease and parasite transmission: Pathogen and parasite transmission increases with host density because contact rates increase.

I. At low density: Disease prevalence low; different disease-resistance genotypes have similar fitness

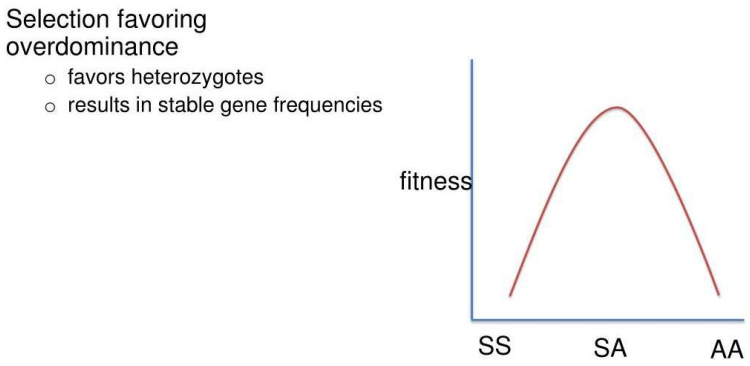
II. At high density: Disease prevalent; disease-resistant genotypes have substantial fitness advantage

Intraspecific aggression and territoriality: At high densities, social stress and aggressive interactions increase, affecting fitness of different phenotypes.

8. Heterozygous Superiority (Overdominance)

8.1 Definition and Concept

Heterozygous superiority (also called **overdominance** or **heterozygote advantage**) occurs when the heterozygous genotype (Aa) has higher fitness than both homozygous genotypes (AA and aa). This creates a balanced polymorphism where both alleles are maintained indefinitely in the population because heterozygotes are the fittest class.



The Sickle Cell Trait Example

One of the clearest examples of heterozygote advantage in humans involves the sickle cell hemoglobin variant:

Genetic basis: Single nucleotide substitution in β-globin gene (GAG→GTG), coding for valine instead of glutamic acid at position 6, causing hemoglobin polymerization under low oxygen.

Fitness values in malaria-endemic regions (West Africa):

Genotype	Phenotype	Fitness	Explanation
AA	Normal	0.88	Susceptible to malaria; reduced survival
AS	Sickle trait	1.00 (highest)	Resistant to malaria; normal blood function
SS	Sickle cell disease	0.14	Severe anemia; high mortality

Why heterozygotes are superior:

Malaria resistance: Heterozygotes have one sickle and one normal allele. Malaria parasites cannot efficiently invade sickled RBCs, providing protection

Normal physiology: Only one allele produces sickling; heterozygotes don't have severe hemolytic anemia

Dual advantage: Heterozygotes gain both malaria resistance AND normal physiology

Evolutionary outcome:

- In malaria-endemic regions: Both S and A alleles maintained; heterozygotes common
- In non-malarial regions: S allele disadvantageous (no malaria benefit; only hemolytic anemia); S allele decreases toward loss
- Equilibrium frequency in West Africa: ~10% for S allele

Why it's a balanced polymorphism:

- Selection against AA (malaria kills many): favours S allele
- Selection against SS (sickle disease kills many): favours A allele
- These opposing forces maintain both alleles indefinitely

9. Kin Selection

9.1 Definition and Theoretical Framework

Kin selection is the evolution of altruistic or cooperative behaviour through selection favouring the reproductive success of genetic relatives, not just direct offspring. Unlike traditional individual selection focusing on personal reproduction, kin selection recognizes that genes can increase evolutionary success by promoting reproduction of close relatives who share those same genes.

9.2 Inclusive Fitness

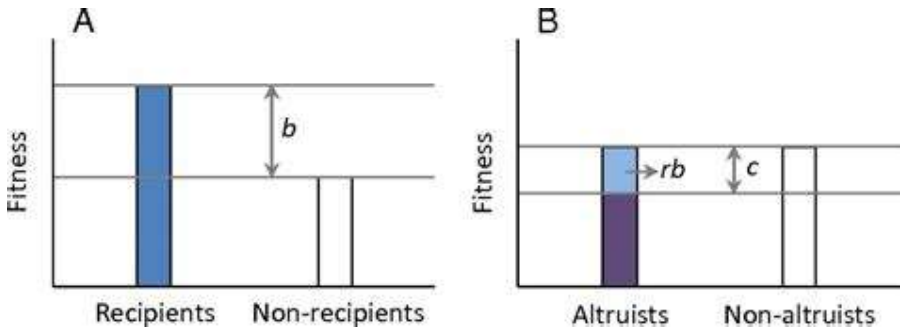
Inclusive fitness extends the concept of fitness to include both direct fitness (personal reproduction) and indirect fitness (effects on relatives' reproduction).

Inclusive fitness = direct fitness + indirect fitness

Or more precisely:

Inclusive fitness = offspring contribution + (relatedness × relatives' offspring contribution)

9.3 Hamilton's Rule



Hamilton's rule provides the mathematical criterion for when altruistic behaviour evolves:

rb - c > 0

Or equivalently: **rb > c**

Where:

r = coefficient of genetic relatedness between altruist and recipient

b = benefit to recipient (in number of offspring equivalents gained)

c = cost to altruist (in number of offspring equivalents lost)

Interpretation:

I. An altruistic allele increases when the benefit to relatives (weighted by relatedness) exceeds the personal reproductive cost

II. The closer the relationship (higher r), the lower the benefit needs to be to favour altruism

III. Conversely, for distantly related individuals, large benefits are needed to overcome personal costs

9.4 Coefficients of Genetic Relatedness

Relatedness (r) represents the probability that a gene in one individual is identical by descent (shared from common ancestor) with a gene in another:

Relationship	r	Explanation
Parent-offspring	0.5	Share 50% of genes
Full sibling	0.5	On average share 50% of genes
Grandparent-grandchild	0.25	Share 25% of genes
Uncle/aunt-niece/nephew	0.25	Share 25% of genes
Cousin	0.125	Share 12.5% of genes
Unrelated	0	Share no genes IBD

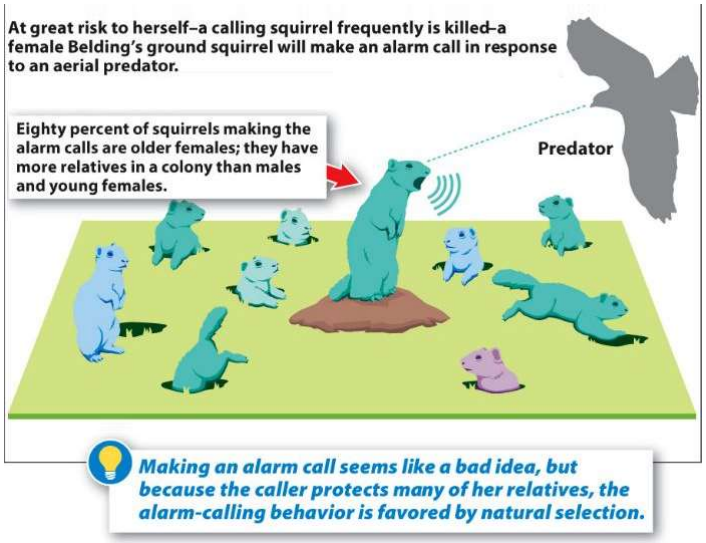
9.5 Example: Alarm Calls in Belding's Ground Squirrels

Behaviour: Sentinels detect predators (hawks, eagles, coyotes) and emit alarm calls, alerting nearby individuals.

Cost to altruist: By calling, the alarm-giver reveals its position to the predator, increasing its personal predation risk.

Benefit to recipients: Relatives hearing the alarm escape to burrows, increasing their survival and reproduction.

Kinship effect: Female ground squirrels with more nearby sisters emit more alarm calls than females with fewer sisters. Squirrels rarely call when only distant relatives are nearby.

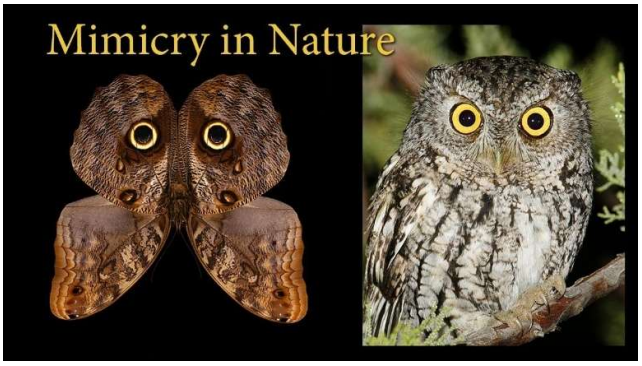


Hamilton's rule explanation:

- For sisters (r = 0.5): Cost of calling is small compared to large benefit to sisters
- rb = 0.5 × (high benefit) > c (calling cost)
- Altruism is favoured
- For distant relatives: rb = 0.125 × (benefit) may not exceed personal cost
- Altruism not favoured for distant relatives

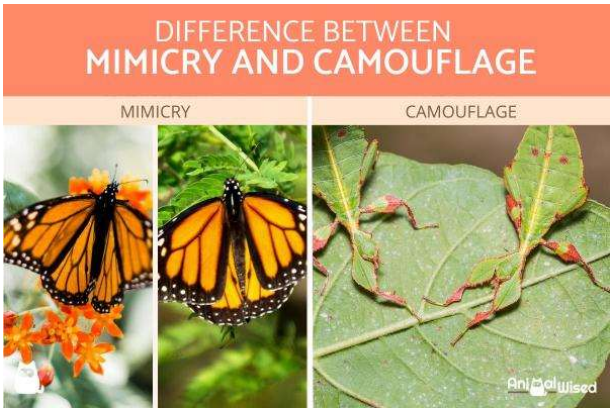
10. Adaptive Resemblances

10.1 Definition and Types



Adaptive resemblances are heritable phenotypic traits that allow organisms to avoid detection or recognition by predators or competitors, thereby increasing survival and reproduction. These resemblances often involve structure, coloration, or behaviour matching or mimicking aspects of the environment or other organisms.

Major categories of adaptive resemblances:



Camouflage (Concealment): Organism's appearance matches its background, making it difficult for predators to detect it.

Mimicry: Organism resembles another, usually unpalatable or dangerous species, gaining protection through confusion or avoidance.

Example: Stick insects

- Morphology: Long, thin body resembles twigs
- Color: Brown or green matching tree bark and leaves
- Behaviour: Remain motionless during daylight hours
- Predators: Birds scan vegetation for moving prey; stationary stick insects are cryptic

11. Sexual Selection

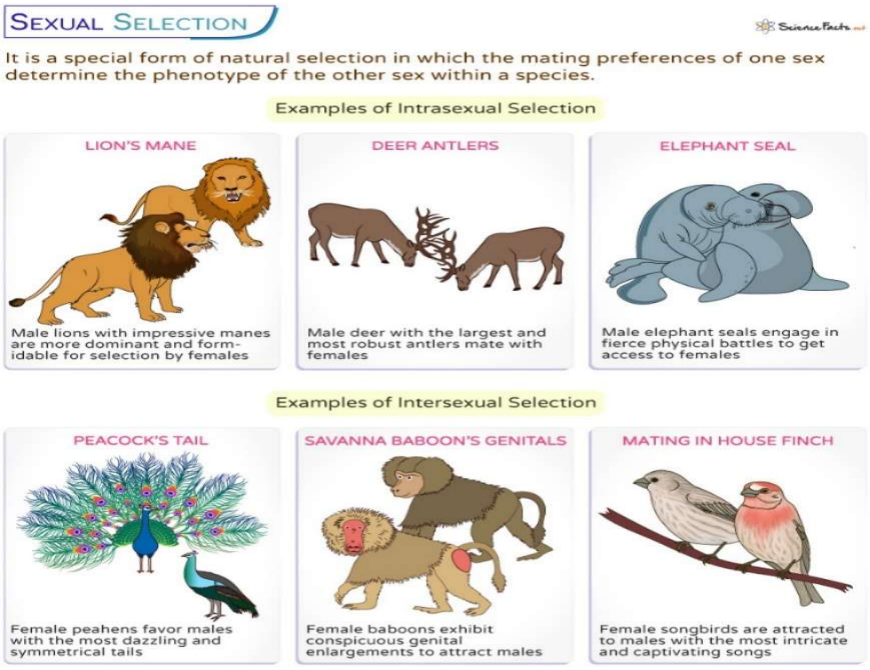
11.1 Definition and Distinction from Natural Selection

Sexual selection occurs when certain individuals achieve greater reproductive success based on their success at acquiring mates or mating, rather than through survival advantages. It's a special form of natural selection focusing on reproductive competition and mate choice rather than survival challenges.

Key difference:

- **Natural selection** on survival traits favours efficiency and functionality (e.g., camouflage, predator evasion)
- **Sexual selection** on mating traits can favour costly, even maladaptive traits (e.g., elaborate tail feathers increasing predation risk)

11.2 Types of Sexual Selection



<u>Intrasexual Selection (Same-sex competition)</u>:

Members of one sex (typically males) compete directly with each other for access to mates or breeding territories.

Mechanisms:

I. Combat/fighting (horns, antlers, body size)

II. Intimidation displays

III. Sperm competition

Result: Evolution of exaggerated weaponry or aggressive displays.

Example: Elephant seals

I. Males compete violently for access to breeding females
II. Sexual dimorphism: Dominant bulls weigh 3,500+ kg while females weigh ~1,000 kg
III. Winners gain reproductive access to harems; losers breed rarely
IV. Selection: Larger, stronger males dominate; size increases through sexual selection despite metabolic costs

Intersexual Selection (Opposite-sex choice):

One sex (typically females) chooses mates based on attractiveness of traits, resources, or genetic quality.

Why females are typically choosy:

I. Higher parental investment: Females invest heavily in gamete production, pregnancy/gestation, lactation
II. Limited breeding opportunities: At any time, fewer females are reproductively available
III. Quality discrimination: Females can identify and select high-quality males
IV. Genetic benefits: Females benefit from choosing males with good genes

Male traits under sexual selection:

I. Ornaments: Elaborate colors, songs, displays (attract females)
II. Resources: Territories, nesting sites (females choosing resource-rich males)
III. Genetic quality indicators: Fitness indicators like parasite resistance

11.3 Sexual Dimorphism

Sexual dimorphism refers to phenotypic differences between males and females beyond reproductive organs. Results from sex-specific selection pressures.

Common patterns:

- Males larger than females (in polygynous species with male-male competition)
- Males with elaborate ornamentation (in species with female choice)
- Males with bright coloration; females dull
- Females larger than males (in some species with female competition or high fecundity demands)

11.4 Examples of Sexual Selection Traits

Elaborate plumage: Birds of paradise (hundreds of plumage variations), pheasants (long tail feathers), peafowl (tail eyespots)

Vocalizations: Songbirds' complex songs, frog calls, whale songs

Displays: Courtship displays (dancing, posturing), threat displays

Secondary sexual characters: Manes (lions), wattles (turkeys), proboscis (proboscis monkeys)

Sperm production: Males evolving huge testes relative to body size in species with sperm competition

11.5 Costs and Benefits of Sexual Selection

Costs of sexual selection:

I. Reduced survival (conspicuous coloration, energetically expensive displays)
II. Reduced mobility (long tail feathers impair flight)
III. Disease susceptibility (immune system allocation trade-offs)
IV. Reduced parental care (male spends energy on display/mating rather than offspring care)

Benefits of sexual selection:

I. Increased mating success and reproductive output
II. Genetic quality in offspring (if females choose high-quality males)
III. Direct benefits (resources, protection from chosen mates)

Evolutionary equilibrium: Sexual selection traits reach equilibrium when costs equal reproductive benefits, typically producing intermediate trait values (not maximally exaggerated traits).