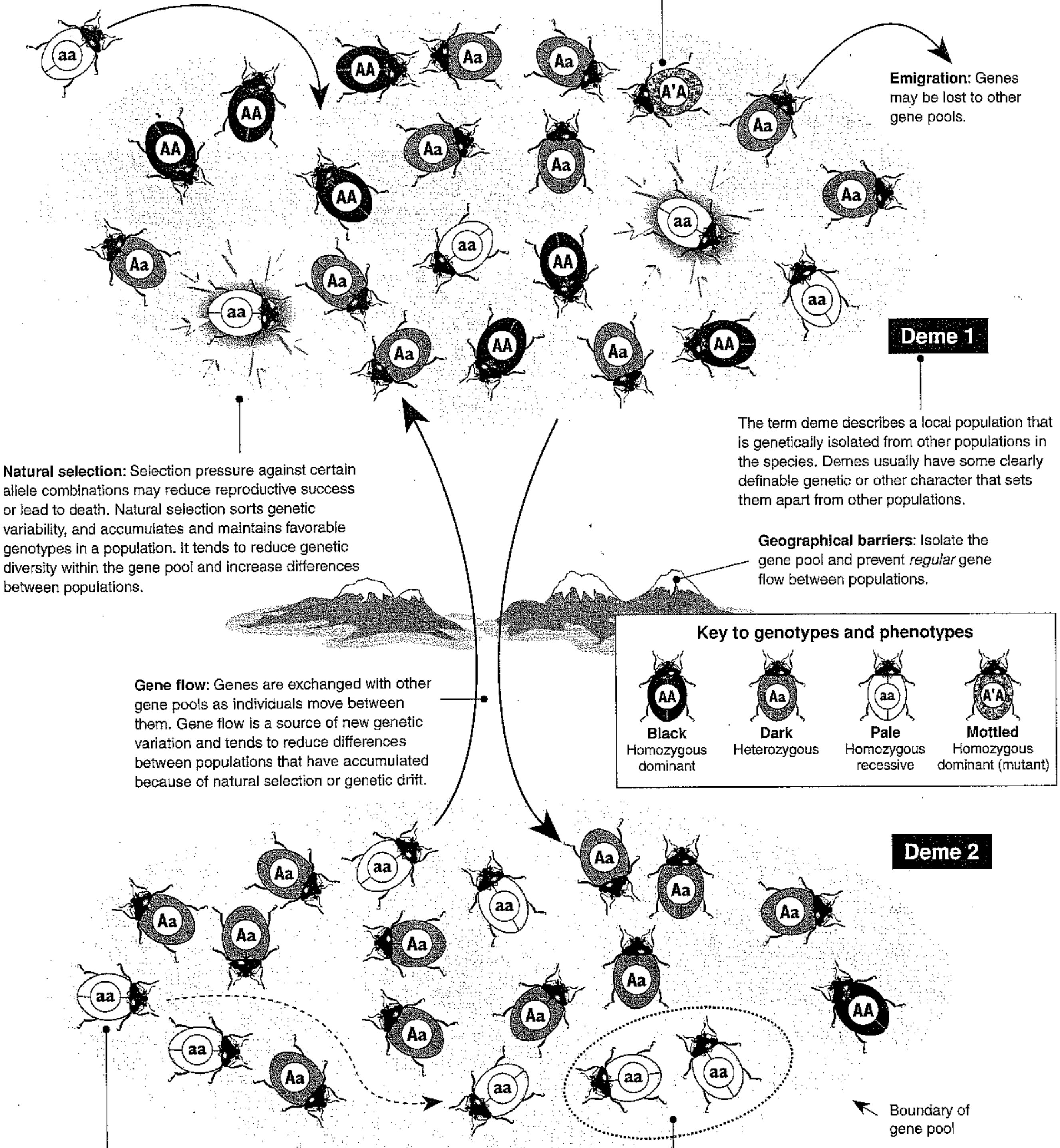
Gene Pools and Evolution

The diagram below illustrates the dynamic nature of **gene pools.** It portrays two imaginary populations of one beetle species. Each beetle is a 'carrier' of genetic information, represented here by the alleles (A and a) for a single **codominant gene** that controls the beetle's color. Normally, there are three versions of the phenotype: black, dark, and pale. Mutations may create other versions of the phenotype. Some of the **microevolutionary processes** that can affect the genetic composition (**allele frequencies**) of the gene pool are illustrated. See the activity *Gene Pool Exercise* for cut-out beetles to simulate this activity.

Mutations: Spontaneous mutations can develop that alter the allele frequencies of the gene pool, and even create new alleles. Mutation is very important to evolution, because it is the original source of genetic variation that provides new material for natural selection.

Immigration: Populations can gain alleles when they are introduced from other gene pools. Immigration is one aspect of gene flow.

Emigration: Genes may be lost to other gene pools.



The term deme describes a local population that is genetically isolated from other populations in the species. Demes usually have some clearly definable genetic or other character that sets them apart from other populations.

Natural selection: Selection pressure against certain allele combinations may reduce reproductive success or lead to death. Natural selection sorts genetic variability, and accumulates and maintains favorable genotypes in a population. It tends to reduce genetic diversity within the gene pool and increase differences between populations.

Geographical barriers: Isolate the gene pool and prevent *regular* gene flow between populations.

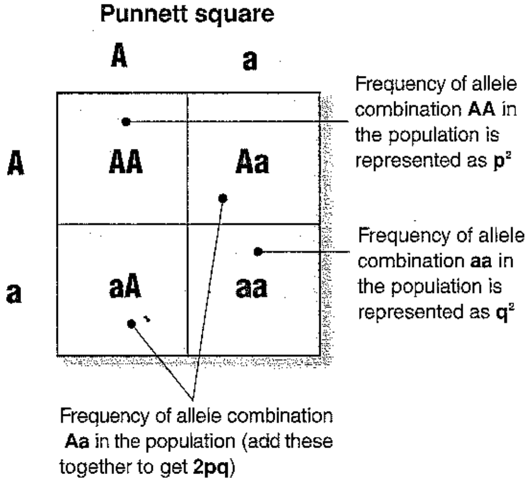
Gene flow: Genes are exchanged with other gene pools as individuals move between them. Gene flow is a source of new genetic variation and tends to reduce differences between populations that have accumulated because of natural selection or genetic drift.

Mate selection (non-random mating): Individuals may not select their mate randomly and may seek out particular phenotypes, increasing the frequency of these "favored" alleles in the population.

Genetic drift: Chance events can cause the allele frequencies of small populations to "drift" (change) randomly from generation to generation. Genetic drift can play a significant role in the microevolution of very small populations. The two situations most often leading to populations small enough for genetic drift to be significant are the **bottleneck effect** (where the population size is dramatically reduced by a catastrophic event) and the **founder effect** (where a small number of individuals colonize a new area).

Population Genetics Calculations

The **Hardy-Weinberg equation** provides a simple mathematical model of genetic equilibrium in a gene pool, but its main application in population genetics is in calculating allele and genotype frequencies in populations, particularly as a means of studying changes and measuring their rate. The use of the Hardy-Weinberg equation is described below.



$$(p + q)^2 = p^2 + 2pq + q^2 = 1$$

Frequency of allele types	Frequency of allele combinations
p = Frequency of allele A	p^2 = Frequency of AA (homozygous dominant)
q = Frequency of allele a	2pq = Frequency of Aa (heterozygous)
	q^2 = Frequency of aa (homozygous recessive)

The Hardy-Weinberg equation is applied to populations with a simple genetic situation: dominant and recessive alleles controlling a single trait. The frequency of all of the dominant (A) and recessive alleles (a) equals the total genetic complement, and adds up to 1 or 100% of the alleles present.

How To Solve Hardy-Weinberg Problems

In most populations, the frequency of two alleles of interest is calculated from the proportion of homozygous recessives (q^2), as this is the only genotype identifiable directly from its phenotype. If only the dominant phenotype is known, q^2 may be calculated (1 – the frequency of the dominant phenotype). The following steps outline the procedure for solving a Hardy-Weinberg problem:

Remember that all calculations must be carried out using proportions, NOT PERCENTAGES!

1. Examine the question to determine what piece of information you have been given about the population. In most cases, this is the percentage or frequency of the homozygous recessive phenotype q^2, or the dominant phenotype $p^2 + 2pq$ (see note above).
2. The first objective is to find out the value of p or q, If this is achieved, then every other value in the equation can be determined by simple calculation.
3. Take the square root of q^2 to find q.
4. Determine p by subtracting q from 1 (i.e. p = 1 – q).
5. Determine p^2 by multiplying p by itself (i.e. p^2 = p x p).
6. Determine 2pq by multiplying p times q times 2.
7. Check that your calculations are correct by adding up the values for $p^2 + q^2 + 2pq$ (the sum should equal 1 or 100%).

Worked example

In the American white population approximately 70% of people can taste the chemical phenylthiocarbamide (PTC) (the dominant phenotype), while 30% are non-tasters (the recessive phenotype).

Determine the frequency of:	***Answers***
(a) Homozygous recessive phenotype(q^2).	30% - provided
(b) The dominant allele (**p**).	45.2%
(c) Homozygous tasters (**p^2**).	20.5%
(d) Heterozygous tasters (**2pq**).	49.5%

Data: The frequency of the dominant phenotype (70% tasters) and recessive phenotype (30% non-tasters) are provided.

Working:

Recessive phenotype: **q^2** = 30%
use 0.30 for calculation

therefore: **q** = 0.5477
square root of 0.30

therefore: **p** = 0.4523
1 – q = p
1 – 0.5477 = 0.4523

Use p and q in the equation (top) to solve any unknown:

Homozygous dominant **p^2** = 0.2046
(p x p = 0.4523 x 0.4523)

Heterozygous: **2pq** = 0.4953

1. A population of hamsters has a gene consisting of 90% M alleles (black) and 10% m alleles (gray). Mating is random.
Data: Frequency of recessive allele (10% m) and dominant allele (90% M).

Determine the proportion of offspring that will be black and the proportion that will be gray (show your working):

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Recessive allele: q =

Dominant allele: p =

Recessive phenotype: q^2 =

Homozygous dominant: p^2 =

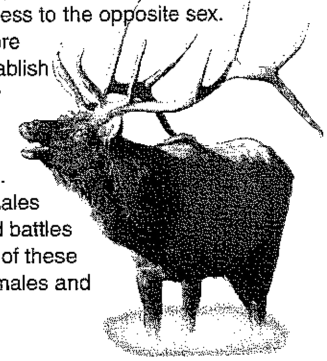
Heterozygous: 2pq =

Sexual Selection

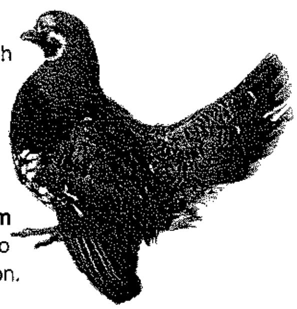
The success of an individual is measured not only by the number of offspring it leaves, but also by the quality or likely reproductive success of those offspring. This means that it becomes important who its mate will be. It was Darwin (1871) who first introduced the concept of sexual selection; a special type of natural selection that produces anatomical and behavioral traits that affect an individual's ability to acquire mates. Biologists today recognise two types: **intrasexual selection** (usually male-male competition) and **intersexual selection** or mate selection. One result of either type is the evolution of **sexual dimorphism**.

Intrasexual Selection

Intrasexual selection involves competition within one sex (usually males) with the winner gaining access to the opposite sex. Competition often takes place before mating, and males compete to establish dominance or secure a territory for breeding or mating. This occurs in many species of ungulates (**deer**, antelope, cattle) and in many birds. In deer and other ungulates, the males typically engage in highly ritualized battles with horns or antlers. The winners of these battles gain dominance over rival males and do most of the mating.

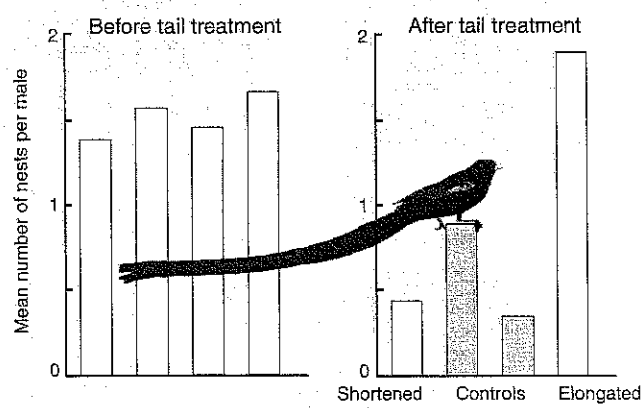


In other species, males compete vigorously for territories. These may contain resources or they may consist of an isolated area within a special arena used for communal courtship display (a **lek**). In lek species, males with the best territories on a lek (the dominant males) are known to get more chances to mate with females. In some species of grouse (right), this form of sexual selection can be difficult to distinguish from intersexual selection, because once males establish their positions on the lek the females then choose among them. In species where there is limited access to females and females are promiscuous, **sperm competition** (below,center) may also be a feature of male-male competition.



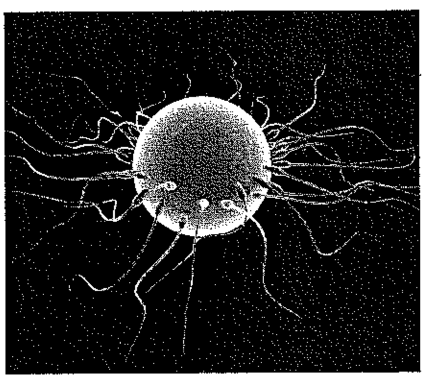
Intersexual Selection

In intersexual selection (or **mate choice**), individuals of one sex (usually the males) advertise themselves as potential mates and members of the other sex (usually the females), choose among them. Intersexual selection results in development of exaggerated ornamentation, such as elaborate plumages. Female preference for elaborate male ornaments is well supported by both anecdotal and experimental evidence. For example, in the **long-tailed widow bird** (*Euplectes progne*), females prefer males with long tails. When tails are artificially shortened or lengthened, females still prefer males with the longest tails; they therefore select for long tails, not another trait correlated with long tails.

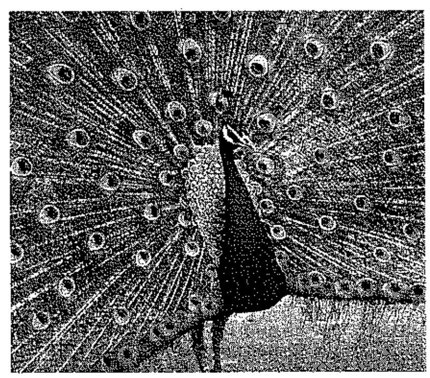


As shown above, there was no significant difference in breeding success between the groups before the tails were altered. When the tails were cut and lengthened, breeding success went down and up respectively.

In male-male competition for mates, ornamentation is used primarily to advertise superiority to rival males, and not to mortally wound opponents. However, injuries do occur, most often between closely matched rivals, where dominance must be tested and established through the aggressive use of their weaponry rather than mere ritual duels.



Sperm competition occurs when females remate within a relatively short space of time. The outcome of sperm competition may be determined by mating order. In some species, including those that guard their mates, the first male has the advantage, but in many the advantage accrues to the sperm of the second or subsequent males.



How do male features, such as the extravagant plumage of the peacock, persist when increasingly elaborate plumage must become detrimental to survival at some point? At first, preference for such traits must confer a survival advantage. Male adornment and female preference then advance together until a stable strategy is achieved.

1. Explain the difference between **intrasexual selection** and **mate selection**, identifying the features associated with each:

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2. Suggest how sexual selection results in marked **sexual dimorphism**: ______________________________

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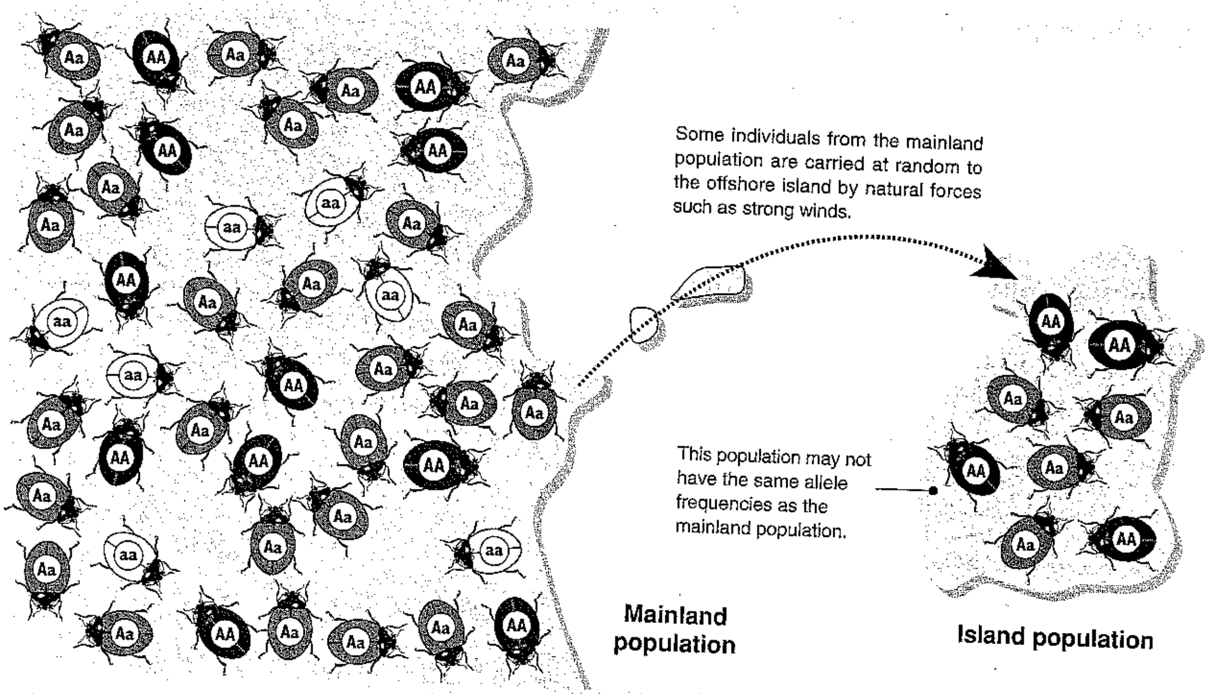
The Founder Effect

Occasionally, a small number of individuals from a large population may migrate away, or become isolated from, their original population. If this colonizing or 'founder' population is made up of only a few individuals, it will probably have a *non-representative sample* of alleles from the parent population's gene pool. As a consequence of this **founder effect**, the colonizing population may evolve differently from that of the parent population, particularly since the environmental conditions for the isolated population may be different. In some cases, it may be possible for certain alleles to be missing altogether from the individuals in the isolated population. Future generations of this population will not have this allele.



Mainland population

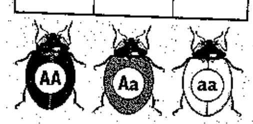
	Allele frequencies: Actual numbers	Allele frequencies: Calculate %
Allele A		
Allele a		
Total		

Phenotype frequencies: Black	Dark	Pale

Colonizing island population

	Allele frequencies: Actual numbers	Allele frequencies: Calculate %
Allele A		
Allele a		
Total		

Phenotype frequencies: Black	Dark	Pale



1. Compare the mainland population to the population which ended up on the island (use the spaces in the tables above):
   (a) Count the **phenotype** numbers for the two populations (i.e. the number of black, dark and pale beetles).
   (b) Count the **allele** numbers for the two populations: the number of dominant alleles (A) and recessive alleles (a). Calculate these as a percentage of the total number of alleles for each population.
2. Describe how the allele frequencies of the two populations are different: ______________________

   ____
3. Describe some possible ways in which various types of organism can be carried to an offshore island:
   (a) Plants: ______________________
   (b) Land animals: ______________________
   (c) Non-marine birds: ______________________
4. Since founder populations are often very small, describe another process that may further alter the allele frequencies:

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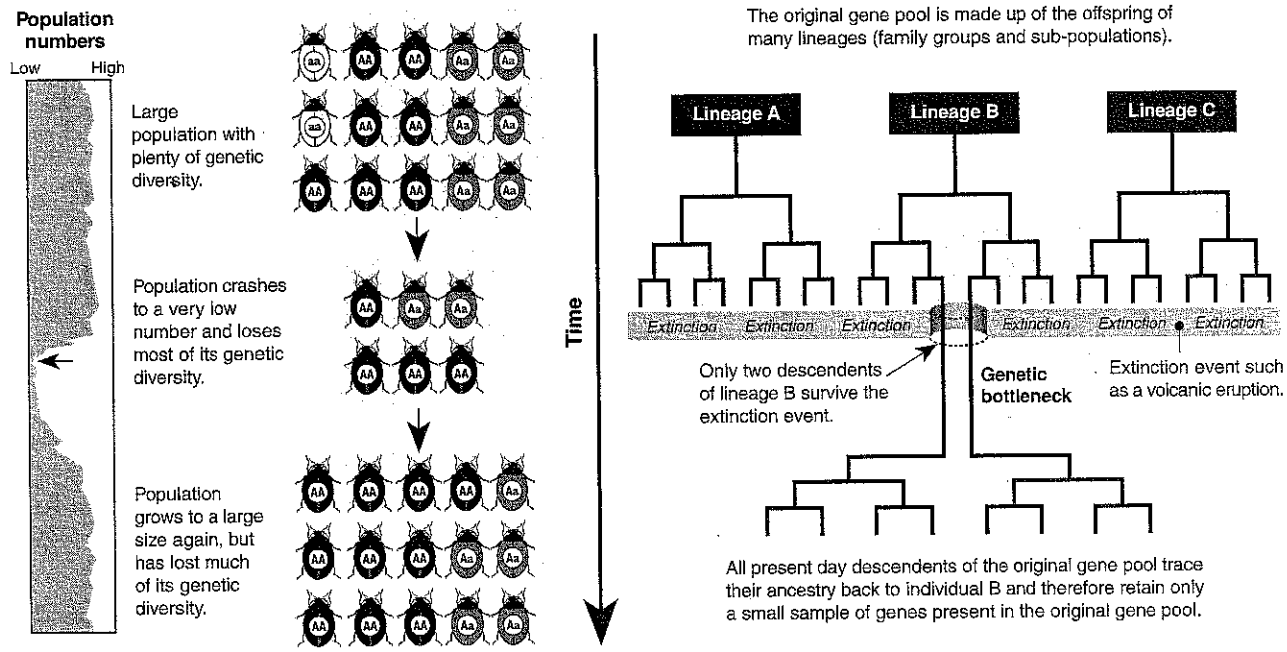
Population Bottlenecks

Populations may sometimes be reduced to low numbers by predation, disease, or periods of climatic change. A population crash may not be 'selective': it may affect all phenotypes equally. Large scale catastrophic events (e.g. fire or volcanic eruption) are examples of such non-selective events. Humans may severely (and selectively) reduce the numbers of some species through hunting and/or habitat destruction. These populations may recover, having squeezed through a 'bottleneck' of low numbers.

The diagram below illustrates how population numbers may be reduced as a result of a catastrophic event. Following such an event, the small number of individuals contributing to the gene pool may not have a representative sample of the alleles in the pre-catastrophe population, i.e. the allele frequencies in the remnant population may be altered. Genetic drift may cause further changes to allele frequencies. The small population may return to previous levels but with a reduced genetic diversity.



Modern Examples of Population Bottlenecks

Cheetahs: The world population of cheetahs currently stands at fewer than 20 000. Recent genetic analysis has found that the entire population enhibits very little genetic diversity. It appears that cheetahs may have narrowly escaped extinction at the end of the last ice age, about 10-20 000 years ago. If all modern cheetahs arose from a very limited genetic stock, this would explain their present lack of genetic diversity. The lack of genetic variation has resulted in a number of problems that threaten cheetah survival, including sperm abnormalities, decreased fecundity, high cub mortality, and sensitivity to disease.

Illinois prairie chicken: When Europeans first arrived in North America, there were millions of prairie chickens. As a result of hunting and habitat loss, the Illinois population of prairie chickens fell from about 100 million in 1900 to fewer than 50 in the 1990s. A comparison of the DNA from birds collected in the mid-twentieth century and DNA from the surviving population indicated that most of the genetic diversity has been lost.

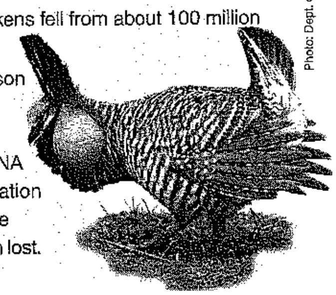


Photo: Dept. of Natural Resources, Illinois

1. Endangered species are often subjected to population bottlenecks. Explain how population bottlenecks affect the ability of a population of an endangered species to recover from its plight:

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2. Explain why the lack of genetic diversity in cheetahs has increased their sensitivity to disease:

____

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3. Describe the effect of a population bottleneck on the potential of a species to adapt to changes (i.e. its ability to evolve):

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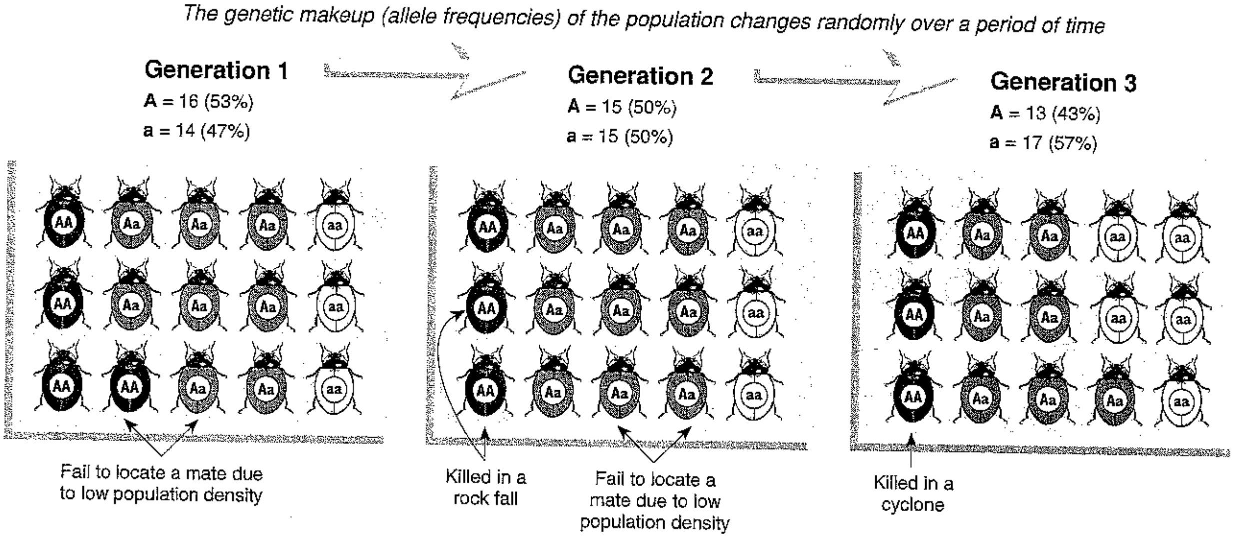
____

Genetic Drift

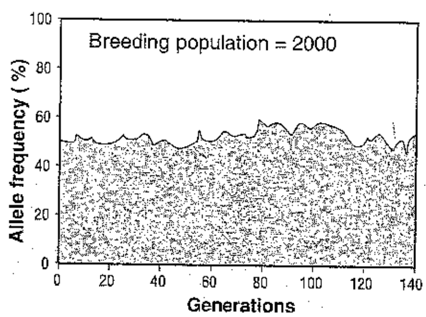
Not all individuals, for various reasons, will be able to contribute their genes to the next generation. **Genetic drift** (also known as the Sewell-Wright Effect) refers to the *random changes in allele frequency* that occur in all populations, but are much more pronounced in small populations. In a small population, the effect of a few individuals not contributing their alleles to the next generation can have a great effect on allele frequencies. Alleles may even become **lost** from the gene pool altogether (frequency becomes 0%) or **fixed** as the only allele for the gene present (frequency becomes 100%).



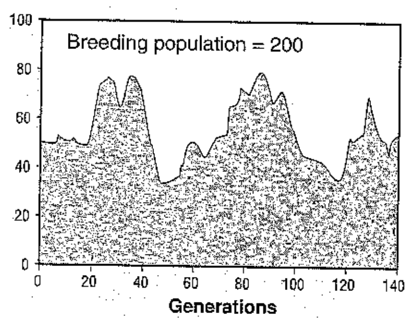
This diagram shows the gene pool of a hypothetical small population over three generations. For various reasons, not all individuals contribute alleles to the next generation. With the random loss of the alleles carried by these individuals, the allele frequency changes from one generation to the next. The change in frequency is directionless as there is no selecting force. The allele combinations for each successive generation are determined by how many alleles of each type are passed on from the preceding one.

Computer Simulation of Genetic Drift

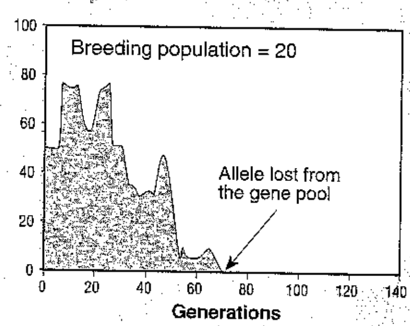
Below are displayed the change in allele frequencies in a computer simulation showing random genetic drift. The breeding population progressively gets smaller from left to right. Each simulation was run for 140 generations.



Large breeding population
Fluctuations are minimal in large breeding populations because the large numbers buffer the population against random loss of alleles. On average, losses for each allele type will be similar in frequency and little change occurs.



Small breeding population
Fluctuations are more severe in smaller breeding populations because random changes in a few alleles cause a greater percentage change in allele frequencies.



Very small breeding population
Fluctuations in very small breeding populations are so extreme that the allele can become fixed (frequency of 100%) or lost from the gene pool altogether (frequency of 0%).

1. Explain what is meant by **genetic drift**: ____________________

2. Describe how genetic drift affects the amount of genetic variation within very small populations: ____________________

3. Identify a small breeding population of animals or plants in your country in which genetic drift could be occurring: ____________________

Reproductive Isolation

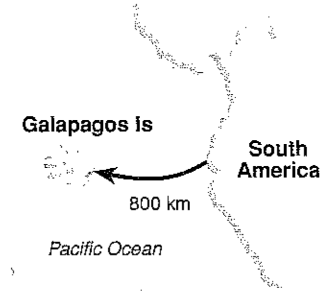
The concept of a biological species is based in **reproductive isolation**, with each species isolated by factors (barriers) that prevent interbreeding (and therefore gene flow) with other species. Any factor that impedes two species from producing viable, fertile hybrids contributes to reproductive isolation. Single barriers may not completely stop gene flow, so most species have more than one type of barrier. Geographical barriers are not always classified as reproductive isolating mechanisms (RIMs) because they are not part of the species' biology. Such barriers often precede the development of other reproductive isolating mechanisms, which can operate before fertilization (prezygotic RIMs) or after fertilization (postzygotic RIMs).

Prezygotic Isolating Mechanisms

Spatial (geographical)

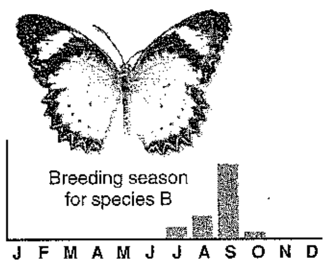
Includes physical barriers such as: mountains, rivers, altitude, oceans, isthmuses, deserts, ice sheets. There are many examples of speciation occurring as a result of isolation by oceans or by geological changes in lake basins (e.g. the proliferation of cichlid fish species in Lake Victoria). The many species of iguana from the Galapagos Islands are now quite distinct from the Central and South American species from which they arose.


Land iguana: Galapagos Is.



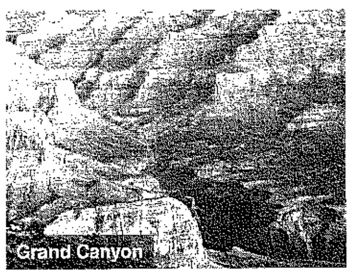
Temporal (including seasonal)

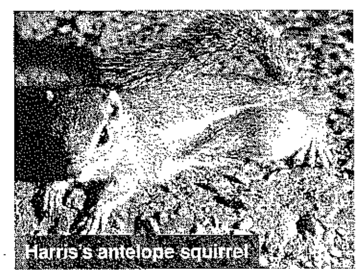
Timing of mating activity for an organism may prevent contact with closely related species: nocturnal, diurnal, spring, summer, fall, spring tide etc. Plants flower at different times of the year or even at different times of the day. Closely related animals may have quite different breeding seasons.



Ecological (habitat)

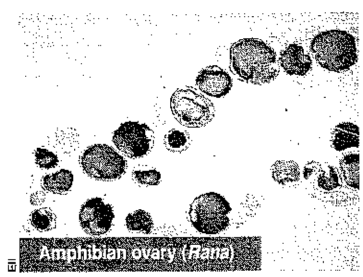
Closely related species may occupy different habitats even within the same general area. In the USA, geographically isolated species of antelope squirrels occupy different ranges either side of the Grand Canyon. The white tailed antelope squirrel inhabits the desert to the north of the canyon, while the smaller Harris's antelope squirrel has a much more limited range to the south of the canyon.

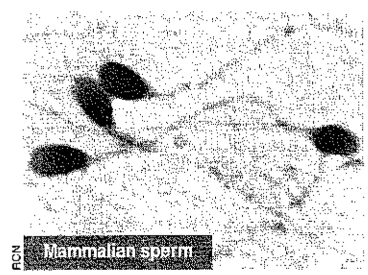

Grand Canyon


Harris's antelope squirrel

Gamete mortality

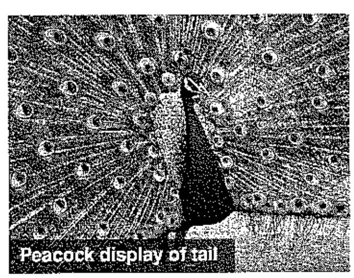
Sperm and egg fail to unite. Even if mating takes place, most gametes will fail to unite. The sperm of one species may not be able to survive in the reproductive tract of another species. Gamete recognition may be based on the presence of species specific molecules on the egg or the egg may not release the correct chemical attractants for sperm of another species.


EII Amphibian ovary (*Rana*)


RCN Mammalian sperm

Behavioral (ethological)

Animals attract mates with calls, rituals, dances, body language, etc. Complex displays, such as the flashes of fireflies, are quite specific. In animals, behavioral responses are a major isolating factor, preserving the integrity of mating within species. Birds exhibit a remarkable range of courtship displays that are often quite species-specific.


Peacock display of tail


Blue footed boobies courtship

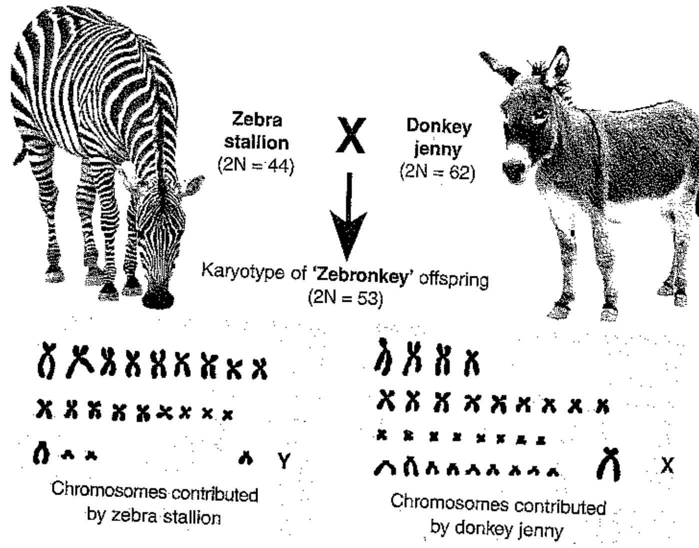
Structural (morphological)

Shape of the copulatory (mating) apparatus, appearance, coloration, insect attractants. Insects have a lock-and-key arrangement for their copulatory organs. Pheromone chemical attractants, which may travel many kilometers with the aid of the wind, are quite specific, attracting only members of the same species.


Beetles mating


Damselflies mating

Postzygotic Isolating Mechanisms

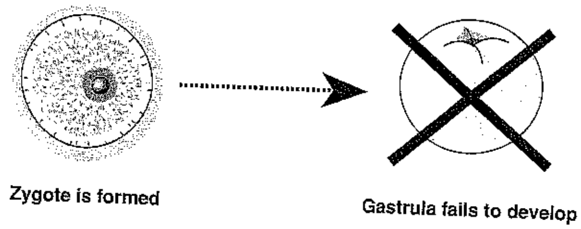


Hybrid sterility

Even if two species mate and produce hybrid offspring that are vigorous, the species are still reproductively isolated if the hybrids are sterile (genes cannot flow from one species' gene pool to the other). Such cases are common among the horse family (such as the zebra and donkey shown on the right). One cause of this sterility is the failure of meiosis to produce normal gametes in the hybrid. This can occur if the chromosomes of the two parents are different in number or structure (see the **"zebronkey"** karyotype on the right). The **mule**, a cross between a donkey stallion and a horse mare, is also an example of **hybrid vigor** (they are robust) as well as **hybrid sterility**. Female mules sometimes produce viable eggs but males are infertile.

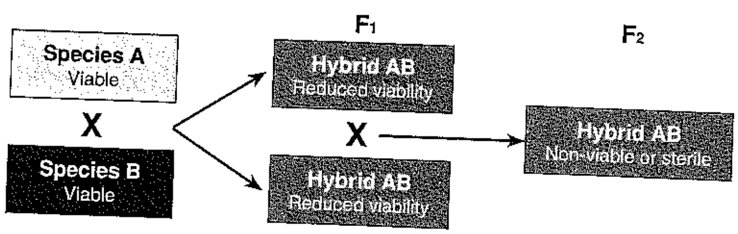
Hybrid inviability

Mating between individuals of two different species may sometimes produce a zygote. In such cases, the genetic incompatibility between the two species may stop development of the fertilized egg at some embryonic stage. Fertilized eggs often fail to divide because of unmatched chromosome numbers from each gamete (a kind of aneuploidy between species). Very occasionally, the hybrid zygote will complete embryonic development but will not survive for long.



Hybrid breakdown

First generation (F_1) are fertile, but the second generation (F_2) are infertile or inviable. Conflict between the genes of two species sometimes manifests itself in the second generation.



1. In general terms, explain the role of reproductive isolating mechanisms in maintaining the integrity of a species:

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2. In the following examples, classify the reproductive isolating mechanism as either **prezygotic** or **postzygotic** and describe the mechanisms by which the isolation is achieved (e.g. temporal isolation, hybrid sterility etc.):

   (a) Some different cotton species can produce fertile hybrids, but breakdown of the hybrid occurs in the next generation when the offspring of the hybrid die in their seeds or grow into defective plants:

   Prezygotic / postzygotic (delete one) Mechanism of isolation: ____________________

   (b) Many plants have unique arrangements of their floral parts that stops transfer of pollen between plants:

   Prezygotic / postzygotic (delete one) Mechanism of isolation: ____________________

   (c) Three species of orchid living in the same rainforest do not hybridize because they flower on different days:

   Prezygotic / postzygotic (delete one) Mechanism of isolation: ____________________

   (d) Several species of the frog genus *Rana*, live in the same regions and habitats, where they may occasionally hybridize. The hybrids generally do not complete development, and those that do are weak and do not survive long:

   Prezygotic / postzygotic (delete one) Mechanism of isolation: ____________________

3. Postzygotic isolating mechanisms are said to reinforce prezygotic ones. Explain why this is the case:

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