9th Grade
Textbook Packet
3/30/2020-4/3/2020

GENETIC EQUILIBRIUM

By the time of Darwin's death, in 1882, the idea of evolution by natural selection had gained wide acceptance among scientists. Within the next century, an increasing scientific understanding of genetics became strongly linked with theories of evolution and natural selection.

SECTION 1

OBJECTIVES

- **Identify** traits that vary in populations and that may be studied.
- **Explain** the importance of the bell curve to population genetics.
- **Compare** three causes of genetic variation in a population.
- **Calculate** allele frequency and phenotype frequency.
- **Explain** Hardy-Weinberg genetic equilibrium.

VOCABULARY

population genetics
microevolution
bell curve
gene pool
allele frequency
phenotype frequency
Hardy-Weinberg genetic equilibrium

VARIATION OF TRAITS WITHIN A POPULATION

Population genetics is the study of evolution from a genetic point of view. Evolution at the genetic level is sometimes called **microevolution,** defined as a change in the collective genetic material of a population. Recall that the genetic material of organisms consists of many alleles—or variations—of many genes that code for various traits. Recall that a population consists of a group of individuals of the same species that routinely interbreed. Populations are important to the study of evolution because a population is the smallest unit in which evolution occurs.

Within a population, individuals may vary in observable traits. For example, fish of a single species in a pond may vary in size. Biologists often study variation in a trait by measuring that trait in a large sample. Figure 16-1 shows a graph of the frequency of lengths in a population of mature fish. Because the shape of the curve looks like a bell, it is called a **bell curve.** The bell curve shows that whereas a few fish in this population are very short and a few are very long, most are of average length. In nature, many quantitative traits in a population—such as height and weight—tend to show variation that follows a bell curve pattern.

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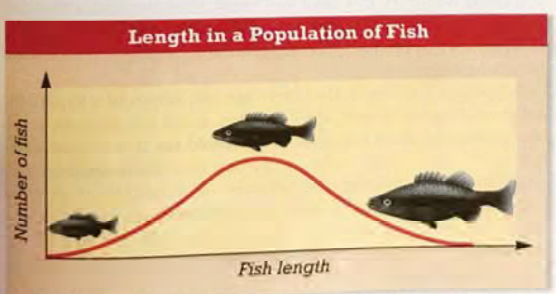


FIGURE 16-1
A bell curve illustrates that most members of a population have similar values for a given, measurable trait. Only a few individuals display extreme variations of the trait.

FIGURE 16-2
Many varied but similar phenotypes occur within families because members of a family share some alleles but not others.

Causes of Variation

What causes variation in traits? Some variations are influenced by environmental factors, such as the amount or quality of food available to an organism. Variation is also influenced by heredity. Some variations occur as a range of phenotypic possibilities (such as a range of body sizes), whereas others occur as a set of specific phenotypes (such as two possible flower colors).

To consider variability, think about phenotypes within a single human family. Two parents, each with a distinct genotype, may produce several children. In the picture of the family in Figure 16-2, the two young-adult brothers are not identical to each other, even though their genotypes are combinations of the genotypes of the same two parents. Both young men resemble their father, though in different traits. The baby resembles his young father, his grandfather, and his uncle. Thus, these males representing three generations look similar but not identical.

What causes genes to vary? Variations in genotype arise in three main ways. (1) *Mutation* is a random change in a gene that is passed on to offspring. (2) *Recombination* is the reshuffling of genes in a diploid individual. Recall that recombination occurs during meiosis by independent assortment and crossing-over of genes on chromosomes. (3) The *random pairing of gametes* occurs because each organism produces large numbers of gametes. So, the union of a particular pair of gametes is partly a matter of chance.

Scientists are still exploring other causes of variation in traits. For example, the expression of some genes depends upon the presence or absence of other genes or factors in the environment. The net result of having many alleles of many genes is the variety of unique genotypes and phenotypes that we see in populations.

THE GENE POOL

Population geneticists use the term **gene pool** to describe the total genetic information available in a population. It is easy to imagine genes for the next generation as existing in an imaginary pool. If you could inventory this pool and know all of the alleles that are present, then you could apply a simple set of rules based on probability theory to predict expected genotypes and their frequencies for the next generation.

Suppose, for example, that there are two alleles of a hypothetical gene, *A* and *a*, in a set of 10 gametes. If half the gametes in the set (5 gametes) carry the allele A, we would say that the *allele frequency* of the *A* allele is 0.5, or 50 percent. **Allele frequency** is determined by dividing the number of a certain allele (five instances of the *A* allele) by the total number of alleles of all types in the population (10 gametes, each with either an *A* or an *a* allele). Remember that a gamete is haploid and therefore carries only one allele for each gene.

Predicting Phenotype

The population of four o'clock flowers, shown in Figure 16-3, illustrates how phenotype can change from generation to generation. Homozygous *RR* flowers are red. Homozygous *rr* flowers are white. Heterozygous *Rr* flowers are pink rather than red, as you might expect. These flowers show incomplete dominance for color, meaning heterozygotes show a trait that falls between the dominant trait and the recessive trait. Thus, homozygotes and heterozygotes can be easily identified by observing the phenotype.

Compare the parent generation with the offspring generation of the four o'clock flowers shown in Figure 16-3. There are equal numbers of plants with the *RR* genotype and the *Rr* genotype in the first generation. You can compute the phenotype frequencies from the figure. A **phenotype frequency** is equal to the number of individuals with a particular phenotype divided by the total number of individuals in the population. Phenotype frequencies in the first generation are 0.5 pink (4 pink plants out of a total of 8 plants), 0.5 red (4 red plants out of a total of 8 plants), and 0.0 white. Recall that allele frequencies are computed using the same principle: the allele frequencies in the first-generation plants are 0.75 *R* (12 *R* alleles out of a total of 16 alleles) and 0.25 *r* (4 *r* alleles out of a total of 16 alleles).

We now can predict the genotypes and phenotypes of the second generation. If a male gamete encounters a female gamete, they will produce a new four o'clock plant whose genotype is the combination of both parental gametes. Thus, an *R* male gamete combined with an *R* female gamete will produce a plant with the *RR* genotype, which has red flowers. According to the laws of probability, the chance of an *R* gamete (a single allele) meeting with another *R* gamete is the arithmetic product of their allele frequencies in the gene pool:

$$\text{frequency of } R \times \text{frequency of } R = \text{frequency of } RR \text{ pair}$$
$$0.75 \times 0.75 = 0.5625$$

The expected frequency of the *rr* genotype is then

$$\text{frequency of } r \times \text{frequency of } r = \text{frequency of } rr \text{ pair}$$
$$0.25 \times 0.25 = 0.0625$$

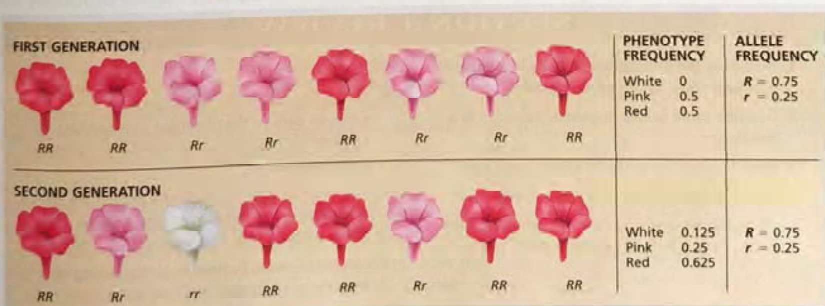


FIGURE 16-3
Although the four o'clock flowers differ phenotypically from generation to generation, the allele frequencies tend to remain the same.

FIGURE 16-4
This flock of mallards, *Anas platyrhynchos*, likely violates some or all of the conditions necessary for Hardy-Weinberg genetic equilibrium.

The frequencies of all genotypes expected in the second generation must add up to 1.0, just as fractions of a whole must add up to 1. Having established the probabilities of getting an *RR* and an *rr* plant, we can compute the expected frequency of the *Rr* plants. All those plants that are neither *RR* nor *rr* will be *Rr*, so

$$1.0 - \text{frequency of } RR - \text{frequency of } rr = \text{frequency of } Rr$$
$$1.0 - 0.5625 - 0.0625 = 0.375$$

HARDY-WEINBERG GENETIC EQUILIBRIUM

It is clear from the example of the four o'clock flowers that phenotype frequencies can change dramatically from generation to generation. But what happens to allele frequencies over generations? A German physician, Wilhelm Weinberg (1862–1937), and a British mathematician, Godfrey Hardy (1877–1947), independently showed that genotype frequencies in a population tend to remain the same from generation to generation unless acted on by outside influences. This principle is referred to as **Hardy-Weinberg genetic equilibrium,** and it is based on a set of assumptions about an ideal hypothetical population that is not evolving:

1. No net mutations occur; that is, the alleles remain the same.
2. Individuals neither enter nor leave the population.
3. The population is large (ideally, infinitely large).
4. Individuals mate randomly.
5. Selection does not occur.

Bear in mind that true genetic equilibrium is a theoretical state. Real populations, such as the flock of mallards in Figure 16-4, may not meet all of the conditions necessary for genetic equilibrium. By providing a model of how genetic equilibrium is maintained, the Hardy-Weinberg principle allows us to consider what forces disrupt genetic equilibrium.

Word Roots and Origins

equilibrium

from the Latin *aequilibris*, meaning "equal balance"

SECTION 1 REVIEW

1. How does the distribution of traits in a population look when displayed as a graph?
2. Describe three causes of genetic variation in a population.
3. What is meant by the term *human gene pool*?
4. How is phenotype frequency computed?
5. What are the conditions that a population must meet in order to have genetic equilibrium?

CRITICAL THINKING

6. **Evaluating Methods** By observation only, is it easier to deduce the genotype of organisms for an allele that has complete dominance or incomplete dominance?
7. **Making Calculations** Half of a population of four o'clocks has red flowers, and half has white flowers. What is the frequency of the *r* allele?
8. **Relating Concepts** How does the pairing of gametes produce genotypic variation?

DISRUPTION OF GENETIC EQUILIBRIUM

Evolution is the change in a population's genetic material over generations, that is, a change of the population's allele frequencies or genotype frequencies. Any exception to the five conditions necessary for Hardy-Weinberg equilibrium can result in evolution.

SECTION 2

OBJECTIVES

- **List** five conditions under which evolution may take place.
- **Explain** how migration can affect the genetics of populations.
- **Explain** how genetic drift can affect populations of different sizes.
- **Contrast** the effects of stabilizing selection, directional selection, and disruptive selection on populations over time.
- **Identify** examples of nonrandom mating.

VOCABULARY

immigration
emigration
gene flow
genetic drift
sexual selection
stabilizing selection
disruptive selection
directional selection

MUTATION

The first requirement for genetic equilibrium is that allele frequencies not change overall because of mutations. Spontaneous mutations occur constantly, at very low rates under normal conditions. But if an organism is exposed to mutagens—mutation-causing agents such as radiation and certain chemicals—mutation rates can increase significantly. Mutations can affect genetic equilibrium by producing totally new alleles for a trait. Many mutations are harmful, although some have no effect. Because natural selection operates only on genes that are expressed, it is very slow to eliminate harmful recessive mutations. In the long run, however, beneficial mutations are a vital part of evolution.

GENE FLOW

The second requirement for genetic equilibrium is that the size of the population remains constant. If individuals move, genes move with them. **Immigration** is the movement of individuals into a population, and **emigration** is the movement of individuals out of a population.

The behavioral ecology of some animal species encourages immigration and emigration. Common baboons live on the savannas of eastern Africa in social and breeding groups called *troops*. A troop is dominated by a few adult males, and it may have from 10 to 200 members. Females tend to remain with the troop they are born into; however, younger or less dominant males leave their birth troop, eventually joining another troop. This constant movement of male animals ensures gene flow. **Gene flow** is the process of genes moving from one population to another. Gene flow can occur through various mechanisms, such as the migration of individuals or the dispersal of seeds or spores.

Word Roots and Origins

immigration

from the Latin *immigrare*, meaning "to go into"

FIGURE 16-5

Genetic drift is significant only in small and medium-sized populations. In a small population, a particular allele may disappear completely over a few generations. In a larger population, a particular allele may vary widely in frequency due to chance but still be present in enough individuals to be maintained in the population. In a much larger population, the frequency of a particular allele may vary slightly by chance but remain relatively stable over generations.

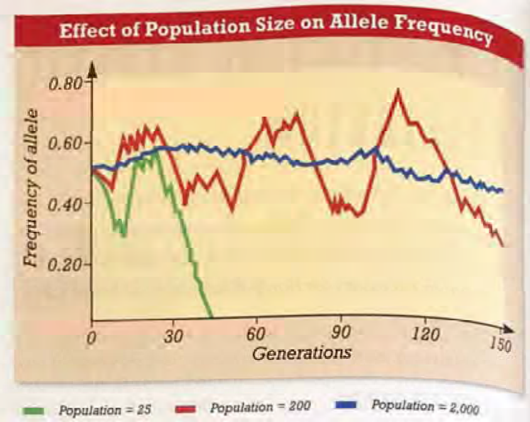


FIGURE 16-6

Populations of the once nearly extinct northern elephant seal, *Mirounga angustirostris*, have lost genetic variability—individuals are homozygous for all of their genes that have been tested. This result of genetic drift could make the species vulnerable to extinction.

GENETIC DRIFT

The third requirement of genetic equilibrium is the presence of a large population. The Hardy-Weinberg principle is based on the laws of probability, which are less applicable to smaller populations. **Genetic drift** is the phenomenon by which allele frequencies in a population change as a result of random events, or chance. In small populations, the failure of even a single organism to reproduce can significantly disrupt the allele frequency of the population, as can greater-than-normal reproduction by an individual, resulting in genetic drift. Because it can result in significant changes within a population, genetic drift is thought to be another possible mechanism for the evolution of new species.

Figure 16-5 shows a graph of genetic drift in populations of three differing sizes. Small populations can undergo abrupt changes in allele frequencies, exhibiting a large degree of genetic drift, whereas large populations retain fairly stable allele frequencies, maintaining a small degree of genetic drift. In the smallest population shown in the graph, the frequency of the example allele reaches zero at about the 45th generation. If we assume that the population started with two alleles for a trait, then only one allele is left, and every individual is homozygous for that trait. Once this change happens, the population is in danger of becoming extinct because there is no variation for natural selection to act on. For example, a natural disaster or a new disease could wipe out the entire population. For this reason, endangered species, such as the northern elephant seal, as shown in Figure 16-6, remain in peril of extinction even as their numbers increase.

NONRANDOM MATING

The fourth requirement of genetic equilibrium is random matings, without regard to genetic makeup. However, many species do not mate randomly. Mate selection is often influenced by geographic proximity, which can result in mates with some degree of kinship. Matings of related individuals can amplify certain traits and can result in offspring with disorders caused by recessive genes, which, although rare, may be present in the genomes of related individuals.

In another example of nonrandom mating, individuals may select a mate that has traits similar to their own traits. This mate would probably have some similar genes. The selection of a mate based on similarity of traits is called *assortative mating*. Nonrandom mating affects which alleles will be combined within individuals, but it does not affect overall allele frequencies within a population.

Sexual Selection

In many species of birds, the males are brightly colored and often heavily plumed, such as the peacock shown in Figure 16-7. These elaborately decorated males are easy for predators to see. Why would natural selection work in favor of an organism being conspicuous to a predator? Females tend to choose the males they mate with based on certain traits. This tendency is referred to as **sexual selection.** In order to leave offspring, a male must be selected by the female. The peacock's gaudy plumage increases his chances of being selected. Extreme traits, such as heavy, brightly colored plumage, may give the female an indication of the quality of the male's genes or his fitness in his environment. Remember that natural selection acts upon differences in survival *and* reproduction. Natural selection favors an increase in the genes of successful *reproducers*, rather than merely those of successful *survivors*.

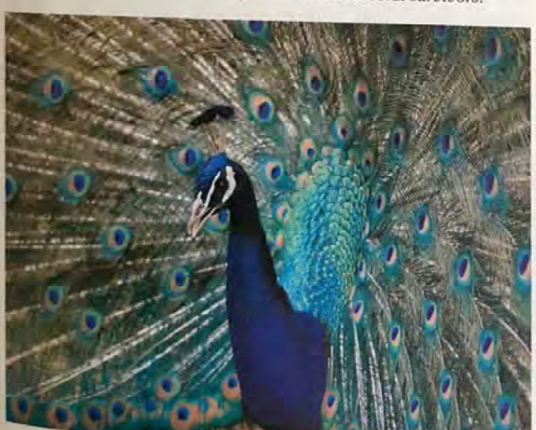


FIGURE 16-7

Males sometimes display extreme traits, such as the large tail of this peacock, *Pavo cristatus*. This trait is favorable if it attracts females and increases the reproductive fitness of the male.

Quick Lab

Evaluating Selection

Materials unlined paper, colored pencils, 25 colored candies

Procedure

1. Fold a sheet of unlined paper in half, top over bottom. Using colored pencils, decorate half the paper with different colored circles. Make each colored circle about the size of a quarter.
2. Scatter your "population" of candies over the undecorated half of the sheet of paper. Count and record how many candies match the background color.
3. Now, scatter the candies over the decorated half of the sheet of paper. Count and record how many candies match the background color.
4. Candies that match the background color are camouflaged. Calculate the ratio of camouflaged candies to uncamouflaged candies in steps 2 and 3.
5. Repeat steps 2–4 two times, and average your results.
6. Exchange paper with another group, and repeat steps 2–5.

Analysis Was your population more successfully camouflaged on the white background or on the colored background? How did color diversity affect your population's success on the colored background? Based on your results, predict which type of selection might increase your population's fitness in a multicolored environment.

NATURAL SELECTION

The fifth requirement of genetic equilibrium is the absence of natural selection. Natural selection is an ongoing process in nature, so it often disrupts genetic equilibrium. As you have learned, natural selection means that some members of a population are more likely than other members to survive and reproduce and thus contribute their genes to the next generation.

Recall that natural selection operates on variations of traits within a population, such as body size or color. When natural selection is at work over time, the distribution of traits in a population may change. In a graph, this kind of change would appear as a shift away from the normal bell curve. Scientists observe three general patterns of natural selection: stabilizing selection, disruptive selection, and directional selection.

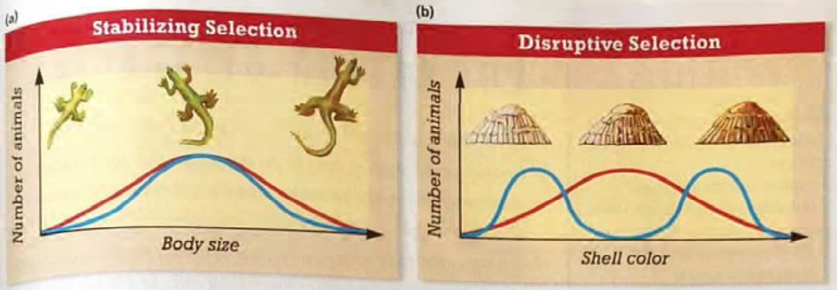
Stabilizing Selection

In **stabilizing selection,** individuals with the average form of a trait have the highest fitness. The average represents the optimum for most traits; extreme forms of most traits confer lower fitness on the individuals that have them. Consider a hypothetical species of lizard in which larger-than-average individuals might be more easily spotted, captured, and eaten by predators. On the other hand, lizards that are smaller than average might not be able to run fast enough to escape.

Figure 16-8a shows the effect of stabilizing selection on body size in these lizards. The red curve shows the initial variation in lizard size as a standard bell curve. The blue curve represents the variation in body size several generations after a new predator was introduced. This predator easily captured the large, visible lizards and the small, slower lizards. Thus, selection against these extreme body types reduced the size range of the lizards. Stabilizing selection is the most common kind of selection. It operates on most traits and results in very similar morphology between most members of a species.

Disruptive Selection

In **disruptive selection,** individuals with either extreme variation of a trait have greater fitness than individuals with the average form of the trait. Figure 16-8b shows the effect of disruptive selection on shell color in limpets, which are marine animals. The shell color of limpets varies from pure white to dark tan. White-shelled limpets that are on rocks covered with goose barnacles, which are also white, are at an advantage. Birds that prey on limpets have a hard time distinguishing the white-shelled limpets from the goose barnacles. On bare, dark-colored rocks, dark-shelled limpets are at an advantage. Again, the limpet-eating birds have a hard time locating the dark shells against the dark background. However, the birds easily spot limpets with shells of intermediate color, which are visible against both the white and dark backgrounds.



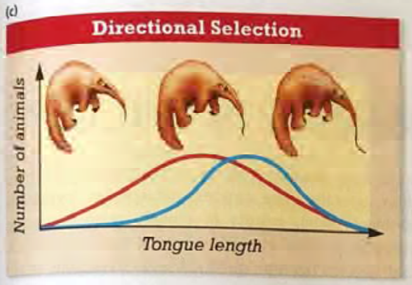


FIGURE 16-8

Natural selection is evident when the distribution of traits in a population changes over time, shifting from the original bell curve (indicated in red) toward another pattern (shown in blue). Stabilizing selection (a) is a shift toward the center of the original bell curve. Disruptive selection (b) is a shift in both directions away from the center. Directional selection (c) is a shift in one direction only.

Directional Selection

In **directional selection,** individuals that display a more extreme form of a trait have greater fitness than individuals with an average form of the trait. Figure 16-8c shows the effects of directional selection on tongue length in anteaters. Anteaters feed by breaking open termite nests, pushing their sticky tongue into the nest, and lapping up termites. Suppose that the termites in an area began to build deeper nests. Anteaters with long tongues could more effectively prey on these termites than could anteaters with short or average tongues. Thus, directional selection would act to direct the trait of tongue length away from the average and toward one extreme.

SECTION 2 REVIEW

1. List five conditions that can disrupt genetic equilibrium and cause evolution to occur.
2. Explain the role of mutations in evolution.
3. Contrast gene flow with genetic drift.
4. Explain why genetic drift is more significant in smaller populations.
5. Contrast stabilizing selection, disruptive selection, and directional selection.

CRITICAL THINKING

6. **Making Inferences** Why might a harmful allele persist in a population for many generations?
7. **Relating Concepts** Give an example of a species that exhibits the effects of sexual selection.
8. **Applying Concepts** For each of the three patterns of natural selection, give an example of a species that exhibits the effects of that selection.

Essential Selections from

The Origin of Species

By Charles Darwin

1. Before applying the principles arrived at in the last chapter to organic beings in a state of nature, we must briefly discuss whether these latter are subject to any variation. To treat this subject at all properly, a long catalogue of dry facts should be given; but these I shall reserve for my future work. Nor shall I here discuss the various definitions which have been given of the term species. No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species. Generally the term includes the unknown element of a distinct act of creation. The term 'variety' is almost equally difficult to define; but here community of descent is almost universally implied, though it can rarely be proved. We have also what are called monstrosities; but they graduate into varieties. By a monstrosity I presume is meant some considerable deviation of structure in one part, either injurious to or not useful to the species, and not generally propagated. Some authors use the term 'variation' in a technical sense, as implying a modification directly due to the physical conditions of life; and 'variations' in this sense are supposed not to be inherited: but who can say that the dwarfed condition of shells in the brackish waters of the Baltic, or dwarfed plants on Alpine summits, or the thicker fur of an animal from far northwards, would not in some cases be inherited for at least some few generations? and in this case I presume that the form would be called a variety.

2. Again, we have many slight differences which may be called individual differences, such as are known frequently to appear in the offspring from the same parents, or which may be presumed to have thus arisen, from being frequently observed in the individuals of the same species inhabiting the same confined locality. No one supposes that all the individuals of the same species are cast in the very same mould. These individual differences are highly important for us, as they afford materials for natural selection to accumulate, in the same manner as man can accumulate in any given direction individual differences in his domesticated productions. These individual differences generally affect what naturalists consider unimportant parts; but I could show by a long catalogue of facts, that parts which must be called important, whether viewed under a physiological or classificatory point of view, sometimes vary in the individuals of the same species. I am convinced that the most experienced naturalist would be surprised at the number of the cases of variability, even in important parts of structure, which he could collect on good authority, as I have collected, during a course of years. It should be remembered that systematists are far from pleased at finding variability in important characters, and that there are not many men who will laboriously examine internal and important organs, and compare them in many specimens of the same species. I should never have expected that the branching of the main nerves close to the great central ganglion of an insect would have been variable in the same species; I should have expected that changes of this nature could have been effected only by slow degrees: yet quite recently Mr Lubbock has shown a degree of variability in these main nerves in Coccus, which may almost be compared to the irregular branching of the stem of a tree. This philosophical naturalist, I may add, has also quite recently shown that the muscles in the larvae of certain insects are very far from uniform. Authors sometimes argue in a circle when they state that important organs never vary; for these same authors practically rank that character as important (as some few naturalists have honestly confessed) which does not vary; and, under this point of view, no instance of any important part varying will ever be found: but under any other point of view many instances assuredly can be given.

3. There is one point connected with individual differences, which seems to me extremely perplexing: I refer to those genera which have sometimes been called 'protean' or 'polymorphic,' in which the species present an inordinate amount of variation; and hardly two naturalists can agree which forms to rank as species and which as varieties. We may instance Rubus, Rosa, and Hieracium amongst plants, several genera of insects, and several genera of Brachiopod shells. In most polymorphic genera some of the species have fixed and definite characters. Genera which are polymorphic in one country seem to be, with some few exceptions, polymorphic in other countries, and likewise, judging from Brachiopod shells, at former periods of time. These facts seem to be very perplexing, for they seem to show that this kind of variability is independent of the conditions of life. I am inclined to suspect that we see in these polymorphic genera variations in points of structure which are of no service or disservice to the species, and which consequently have not been seized on and rendered definite by natural selection, as hereafter will be explained.

4. Those forms which possess in some considerable degree the character of species, but which are so closely similar to some other forms, or are so closely linked to them by intermediate gradations, that naturalists do not like to rank them as distinct species, are in several respects the most important for us. We have every reason to believe that many of these doubtful and closely-allied forms have permanently retained their characters in their own country for a long time; for as long, as far as we know, as have good and true species. practically, when a naturalist can unite two forms together by others having intermediate characters, he treats the one as a variety of the other, ranking the

most common, but sometimes the one first described, as the species, and the other as the variety. But cases of great difficulty, which I will not here enumerate, sometimes occur in deciding whether or not to rank one form as a variety of another, even when they are closely connected by intermediate links; nor will the commonly-assumed hybrid nature of the intermediate links always remove the difficulty. In very many cases, however, one form is ranked as a variety of another, not because the intermediate links have actually been found, but because analogy leads the observer to suppose either that they do now somewhere exist, or may formerly have existed; and here a wide door for the entry of doubt and conjecture is opened.

5. Hence, in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow. We must, however, in many cases, decide by a majority of naturalists, for few well-marked and well-known varieties can be named which have not been ranked as species by at least some competent judges.

6. That varieties of this doubtful nature are far from uncommon cannot be disputed. Compare the several floras of Great Britain, of France or of the United States, drawn up by different botanists, and see what a surprising number of forms have been ranked by one botanist as good species, and by another as mere varieties. Mr H. C. Watson, to whom I lie under deep obligation for assistance of all kinds, has marked for me 182 British plants, which are generally considered as varieties, but which have all been ranked by botanists as species; and in making this list he has omitted many trifling varieties, but which nevertheless have been ranked by some botanists as species, and he has entirely omitted several highly polymorphic genera. Under genera, including the most polymorphic forms, Mr Babington gives 251 species, whereas Mr Bentham gives only 112, a difference of 139 doubtful forms! Amongst animals which unite for each birth, and which are highly locomotive, doubtful forms, ranked by one zoologist as a species and by another as a variety, can rarely be found within the same country, but are common in separated areas. How many of those birds and insects in North America and Europe, which differ very slightly from each other, have been ranked by one eminent naturalist as undoubted species, and by another as varieties, or, as they are often called, as geographical races! Many years ago, when comparing, and seeing others compare, the birds from the separate islands of the Galapagos Archipelago, both one with another, and with those from the American mainland, I was much struck how entirely vague and arbitrary is the distinction between species and varieties. On the islets of the little Madeira group there are many insects which are characterized as varieties in Mr Wollaston's admirable work, but which it cannot be doubted would be ranked as distinct species by many entomologists. Even Ireland has a few animals, now generally regarded as varieties, but which have been ranked as species by some zoologists. Several most experienced ornithologists consider our British red grouse as only a strongly-marked race of a Norwegian species, whereas the greater number rank it as an undoubted species peculiar to Great Britain. A wide distance between the homes of two doubtful forms leads many naturalists to rank both as distinct species; but what distance, it has been well asked, will suffice? if that between America and Europe is ample, will that between the Continent and the Azores, or Madeira, or the Canaries, or Ireland, be sufficient? It must be admitted that many forms, considered by highly-competent judges as varieties, have so perfectly the character of species that they are ranked by other highly-competent judges as good and true species. But to discuss whether they are rightly called species or varieties, before any definition of these terms has been generally accepted, is vainly to beat the air.

7. Many of the cases of strongly-marked varieties or doubtful species well deserve consideration; for several interesting lines of argument, from geographical distribution, analogical variation, hybridism, &c., have been brought to bear on the attempt to determine their rank. I will here give only a single instance, the well-known one of the primrose and cowslip, or Primula veris and elatior. These plants differ considerably in appearance; they have a different flavour and emit a different odour; they flower at slightly different periods; they grow in somewhat different stations; they ascend mountains to different heights; they have different geographical ranges; and lastly, according to very numerous experiments made during several years by that most careful observer Gärtner, they can be crossed only with much difficulty. We could hardly wish for better evidence of the two forms being specifically distinct. On the other hand, they are united by many intermediate links, and it is very doubtful whether these links are hybrids; and there is, as it seems to me, an overwhelming amount of experimental evidence, showing that they descend from common parents, and consequently must be ranked as varieties.

8. Close investigation, in most cases, will bring naturalists to an agreement how to rank doubtful forms. Yet it must be confessed, that it is in the best-known countries that we find the greatest number of forms of doubtful value. I have been struck with the fact, that if any animal or plant in a state of nature be highly useful to man, or from any cause closely attract his attention, varieties of it will almost universally be found recorded. These varieties, moreover, will be often ranked by some authors as species. Look at the common oak, how closely it has been studied; yet a German author makes more than a dozen species out of forms, which are very generally considered as varieties; and in this country the highest botanical authorities and practical men can be quoted to show that the sessile and pedunculated oaks are either good and distinct species or mere varieties.

9. When a young naturalist commences the study of a group of organisms quite unknown to him, he is at first much perplexed to determine what differences to consider as specific, and what as varieties; for he knows nothing of the amount and kind of variation to which the group is subject; and this shows, at least, how very generally there is some variation. But if he confine his attention to one class within one country, he will soon make up his mind how to rank most of the doubtful forms. His general tendency will be to make many species, for he will become impressed, just like the pigeon or poultry-fancier before alluded to, with the amount of difference in the forms which he is continually studying; and he has little general knowledge of analogical variation in other groups and in other countries, by which to correct his first impressions. As he extends the range of his observations, he will meet with more cases of difficulty; for he will encounter a greater number of closely-allied forms. But if his observations be widely extended, he will in the end generally be enabled to make up his own mind which to call varieties and which species; but he will succeed in this at the expense of admitting much variation, and the truth of this admission will often be disputed by other naturalists. When, moreover, he comes to study allied forms brought from countries not now continuous, in which case he can hardly hope to find the intermediate links between his doubtful forms, he will have to trust almost entirely to analogy, and his difficulties will rise to a climax.

10. Certainly no clear line of demarcation has as yet been drawn between species and sub-species that is, the forms which in the opinion of some naturalists come very near to, but do not quite arrive at the rank of species; or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. These differences blend into each other in an insensible series; and a series impresses the mind with the idea of an actual passage.

11. Hence I look at individual differences, though of small interest to the systematist, as of high importance for us, as being the first step towards such slight varieties as are barely thought worth recording in works on natural history. And I look at varieties which are in any degree more distinct and permanent, as steps leading to more strongly marked and more permanent varieties; and at these latter, as leading to sub-species, and to species. The passage from one stage of difference to another and higher stage may be, in some cases, due merely to the long-continued action of different physical conditions in two different regions; but I have not much faith in this view; and I attribute the passage of a variety, from a state in which it differs very slightly from its parent to one in which it differs more, to the action of natural selection in accumulating (as will hereafter be more fully explained) differences of structure in certain definite directions. Hence I believe a well-marked variety may be justly called an incipient species; but whether this belief be justifiable must be judged of by the general weight of the several facts and views given throughout this work.

12. It need not be supposed that all varieties or incipient species necessarily attain the rank of species. They may whilst in this incipient state become extinct, or they may endure as varieties for very long periods, as has been shown to be the case by Mr Wollaston with the varieties of certain fossil land-shells in Madeira. If a variety were to flourish so as to exceed in numbers the parent species, it would then rank as the species, and the species as the variety; or it might come to supplant and exterminate the parent species; or both might co-exist, and both rank as independent species. But we shall hereafter have to return to this subject.

13. From these remarks it will be seen that I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, and for mere convenience sake.

14. Guided by theoretical considerations, I thought that some interesting results might be obtained in regard to the nature and relations of the species which vary most, by tabulating all the varieties in several well-worked floras. At first this seemed a simple task; but Mr H. C. Watson, to whom I am much indebted for valuable advice and assistance on this subject, soon convinced me that there were many difficulties, as did subsequently Dr Hooker, even in stronger terms. I shall reserve for my future work the discussion of these difficulties, and the tables themselves of the proportional numbers of the varying species. Dr Hooker permits me to add, that after having carefully read my manuscript, and examined the tables, he thinks that the following statements are fairly well established. The whole subject, however, treated as it necessarily here is with much brevity, is rather perplexing, and allusions cannot be avoided to the 'struggle for existence,' 'divergence of character,' and other questions, hereafter to be discussed.

15. Alph. De Candolle and others have shown that plants which have very wide ranges generally present varieties; and this might have been expected, as they become exposed to diverse physical conditions, and as they come into competition (which, as we shall hereafter see, is a far more important circumstance) with different sets of organic beings. But my tables further show that, in any limited country, the species which are most common, that is abound most in individuals, and the species which are most widely diffused within their own country (and this is a different consideration from wide range, and to a certain extent from commonness), often give rise to varieties sufficiently well-marked to have been recorded in botanical works.

Hence it is the most flourishing, or, as they may be called, the dominant species, those which range widely over the world, are the most diffused in their own country, and are the most numerous in individuals, which oftenest produce well-marked varieties, or, as I consider them, incipient species. And this, perhaps, might have been anticipated; for, as varieties, in order to become in any degree permanent, necessarily have to struggle with the other inhabitants of the country, the species which are already dominant will be the most likely to yield offspring which, though in some slight degree modified, will still inherit those advantages that enabled their parents to become dominant over their compatriots.

16. If the plants inhabiting a country and described in any Flora be divided into two equal masses, all those in the larger genera being placed on one side, and all those in the smaller genera on the other side, a somewhat larger number of the very common and much diffused or dominant species will be found on the side of the larger genera. This, again, might have been anticipated; for the mere fact of many species of the same genus inhabiting any country, shows that there is something in the organic or inorganic conditions of that country favourable to the genus; and, consequently, we might have expected to have found in the larger genera, or those including many species, a large proportional number of dominant species. But so many causes tend to obscure this result, that I am surprised that my tables show even a small majority on the side of the larger genera. I will here allude to only two causes of obscurity. Fresh-water and salt-loving plants have generally very wide ranges and are much diffused, but this seems to be connected with the nature of the stations inhabited by them, and has little or no relation to the size of the genera to which the species belong. Again, plants low in the scale of organisation are generally much more widely diffused than plants higher in the scale; and here again there is no close relation to the size of the genera. The cause of lowly-organised plants ranging widely will be discussed in our chapter on geographical distribution.

17. From looking at species as only strongly-marked and well-defined varieties, I was led to anticipate that the species of the larger genera in each country would oftener present varieties, than the species of the smaller genera; for wherever many closely related species (*i.e.* species of the same genus) have been formed, many varieties or incipient species ought, as a general rule, to be now forming. Where many large trees grow, we expect to find saplings. Where many species of a genus have been formed through variation, circumstances have been favourable for variation; and hence we might expect that the circumstances would generally be still favourable to variation. On the other hand, if we look at each species as a special act of creation, there is no apparent reason why more varieties should occur in a group having many species, than in one having few.

18. To test the truth of this anticipation I have arranged the plants of twelve countries, and the coleopterous insects of two districts, into two nearly equal masses, the species of the larger genera on one side, and those of the smaller genera on the other side, and it has invariably proved to be the case that a larger proportion of the species on the side of the larger genera present varieties, than on the side of the smaller genera. Moreover, the species of the large genera which present any varieties, invariably present a larger average number of varieties than do the species of the small genera. Both these results follow when another division is made, and when all the smallest genera, with from only one to four species, are absolutely excluded from the tables. These facts are of plain signification on the view that species are only strongly marked and permanent varieties; for whenever many species of the same genus have been formed, or where, if we may use the expression, the manufactory of species has been active, we ought generally to find the manufactory still in action, more especially as we have every reason to believe the process of manufacturing new species to be a slow one. And this certainly is the case, if varieties be looked at as incipient species; for my tables clearly show as a general rule that, wherever many species of a genus have been formed, the species of that genus present a number of varieties, that is of incipient species, beyond the average. It is not that all large genera are now varying much, and are thus increasing in the number of their species, or that no small genera are now varying and increasing; for if this had been so, it would have been fatal to my theory; inasmuch as geology plainly tells us that small genera have in the lapse of time often increased greatly in size; and that large genera have often come to their maxima, declined, and disappeared. All that we want to show is, that where many species of a genus have been formed, on an average many are still forming; and this holds good.

19. There are other relations between the species of large genera and their recorded varieties which deserve notice. We have seen that there is no infallible criterion by which to distinguish species and well-marked varieties; and in those cases in which intermediate links have not been found between doubtful forms, naturalists are compelled to come to a determination by the amount of difference between them, judging by analogy whether or not the amount suffices to raise one or both to the rank of species. Hence the amount of difference is one very important criterion in settling whether two forms should be ranked as species or varieties. Now Fries has remarked in regard to plants, and Westwood in regard to insects, that in large genera the amount of difference between the species is often exceedingly small. I have endeavoured to test this numerically by averages, and, as far as my imperfect results go, they always confirm the view. I have also consulted some sagacious and most experienced observers, and, after deliberation, they concur in this view. In this respect, therefore, the species of the larger genera resemble varieties, more than do the species of the smaller genera. Or the case may be put in another way, and it may be said, that in the larger genera,

in which a number of varieties or incipient species greater than the average are now manufacturing, many of the species already manufactured still to a certain extent resemble varieties, for they differ from each other by a less than usual amount of difference.

20. Moreover, the species of the large genera are related to each other, in the same manner as the varieties of any one species are related to each other. No naturalist pretends that all the species of a genus are equally distinct from each other; they may generally be divided into sub-genera, or sections, or lesser groups. As Fries has well remarked, little groups of species are generally clustered like satellites around certain other species. And what are varieties but groups of forms, unequally related to each other, and clustered round certain forms that is, round their parent-species? Undoubtedly there is one most important point of difference between varieties and species; namely, that the amount of difference between varieties, when compared with each other or with their parent-species, is much less than that between the species of the same genus. But when we come to discuss the principle, as I call it, of Divergence of Character, we shall see how this may be explained, and how the lesser differences between varieties will tend to increase into the greater differences between species.

21. There is one other point which seems to me worth notice. Varieties generally have much restricted ranges: this statement is indeed scarcely more than a truism, for if a variety were found to have a wider range than that of its supposed parent-species, their denominations ought to be reversed. But there is also reason to believe, that those species which are very closely allied to other species, and in so far resemble varieties, often have much restricted ranges. For instance, Mr H. C. Watson has marked for me in the well-sifted London Catalogue of plants (4th edition) 63 plants which are therein ranked as species, but which he considers as so closely allied to other species as to be of doubtful value: these 63 reputed species range on an average over 6.9 of the provinces into which Mr Watson has divided Great Britain. Now, in this same catalogue, 53 acknowledged varieties are recorded, and these range over 7.7 provinces; whereas, the species to which these varieties belong range over 14.3 provinces. So that the acknowledged varieties have very nearly the same restricted average range, as have those very closely allied forms, marked for me by Mr Watson as doubtful species, but which are almost universally ranked by British botanists as good and true species.

22. Finally, then, varieties have the same general characters as species, for they cannot be distinguished from species, except, firstly, by the discovery of intermediate linking forms, and the occurrence of such links cannot affect the actual characters of the forms which they connect; and except, secondly, by a certain amount of difference, for two forms, if differing very little, are generally ranked as varieties, notwithstanding that intermediate linking forms have not been discovered; but the amount of difference considered necessary to give to two forms the rank of species is quite indefinite. In genera having more than the average number of species in any country, the species of these genera have more than the average number of varieties. In large genera the species are apt to be closely, but unequally, allied together, forming little clusters round certain species. Species very closely allied to other species apparently have restricted ranges. In all these several respects the species of large genera present a strong analogy with varieties. And we can clearly understand these analogies, if species have once existed as varieties, and have thus originated: whereas, these analogies are utterly inexplicable if each species has been independently created.

23. We have, also, seen that it is the most flourishing and dominant species of the larger genera which on an average vary most; and varieties, as we shall hereafter see, tend to become converted into new and distinct species. The larger genera thus tend to become larger; and throughout nature the forms of life which are now dominant tend to become still more dominant by leaving many modified and dominant descendants. But by steps hereafter to be explained, the larger genera also tend to break up into smaller genera. And thus, the forms of life throughout the universe become divided into groups subordinate to groups.

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24. Before entering on the subject of this chapter, I must make a few preliminary remarks, to show how the struggle for existence bears on Natural Selection. It has been seen in the last chapter that amongst organic beings in a state of nature there is some individual variability; indeed I am not aware that this has ever been disputed. It is immaterial for us whether a multitude of doubtful forms be called species or sub-species or varieties; what rank, for instance, the two or three hundred doubtful forms of British plants are entitled to hold, if the existence of any well-marked varieties be admitted. But the mere existence of individual variability and of some few well-marked varieties, though necessary as the foundation for the work, helps us but little in understanding how species arise in nature. How have all those exquisite adaptations of one part of the organisation to another part, and to the conditions of life, and of one distinct organic being to another being, been perfected? We see these beautiful co-adaptations most plainly in the woodpecker and missletoe; and only a little less plainly in the humblest parasite which clings to the hairs of a quadruped or feathers of a bird; in the structure of the beetle which dives through the water; in the plumed seed which is wafted by the gentlest breeze; in short, we see beautiful adaptations everywhere and in every part of the organic world.

25. Again, it may be asked, how is it that varieties, which I have called incipient species, become ultimately converted into good and distinct species, which in most cases obviously differ from each other far more than do the varieties of the same species? How do those groups of species, which constitute what are called distinct genera, and which differ from each other more than do the species of the same genus, arise? All these results, as we shall more fully see in the next chapter, follow inevitably from the struggle for life. Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive. I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection. We have seen that man by selection can certainly produce great results, and can adapt organic beings to his own uses, through the accumulation of slight but useful variations, given to him by the hand of Nature. But Natural Selection, as we shall hereafter see, is a power incessantly ready for action, and is as immeasurably superior to man's feeble efforts, as the works of Nature are to those of Art.

26. We will now discuss in a little more detail the struggle for existence. In my future work this subject shall be treated, as it well deserves, at much greater length. The elder De Candolle and Lyell have largely and philosophically shown that all organic beings are exposed to severe competition. In regard to plants, no one has treated this subject with more spirit and ability than W. Herbert, Dean of Manchester, evidently the result of his great horticultural knowledge. Nothing is easier than to admit in words the truth of the universal struggle for life, or more difficult at least I have found it so than constantly to bear this conclusion in mind. Yet unless it be thoroughly engrained in the mind, I am convinced that the whole economy of nature, with every fact on distribution, rarity, abundance, extinction, and variation, will be dimly seen or quite misunderstood. We behold the face of nature bright with gladness, we often see superabundance of food; we do not see, or we forget, that the birds which are idly singing round us mostly live on insects or seeds, and are thus constantly destroying life; or we forget how largely these songsters, or their eggs, or their nestlings are destroyed by birds and beasts of prey; we do not always bear in mind, that though food may be now superabundant, it is not so at all seasons of each recurring year.

27. I should premise that I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny. Two canine animals in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought, 202
though more properly it should be said to be dependent on the moisture. A plant which annually produces a thousand seeds, of which on an average only one comes to maturity, may be more truly said to struggle with the plants of the same and other kinds which already clothe the ground. The missletoe is dependent on the apple and a few other trees, but can only in a far-fetched sense be said to struggle with these trees, for if too many of these parasites grow on the same tree, it will languish and die. But several seedling missletoes, growing close together on the same branch, may more truly be said to struggle with each other. As the missletoe is disseminated by birds, its existence depends on birds; and it may metaphorically be said to struggle with other fruit-bearing plants, in order to tempt birds to devour and thus disseminate its seeds rather than those of other plants. In these several senses, which pass into each other, I use for convenience sake the general term of struggle for existence.

28. A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms; for in this case there can be no artificial increase of food, and no prudential restraint from marriage. Although some species may be now increasing, more or less rapidly, in numbers, all cannot do so, for the world would not hold them.

29. There is no exception to the rule that every organic being naturally increases at so high a rate, that if not destroyed, the earth would soon be covered by the progeny of a single pair. Even slow-breeding man has doubled in twenty-five years, and at this rate, in a few thousand years, there would literally not be standing room for his progeny. Linnaeus has calculated that if an annual plant produced only two seeds and there is no plant so unproductive as this and their seedlings next year produced two, and so on, then in twenty years there would be a million plants. The elephant is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase: it will be under the mark to assume that it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth three pairs of young in this

interval; if this be so, at the end of the fifth century there would be alive fifteen million elephants, descended from the first pair.

30. But we have better evidence on this subject than mere theoretical calculations, namely, the numerous recorded cases of the astonishingly rapid increase of various animals in a state of nature, when circumstances have been favourable to them during two or three following seasons. Still more striking is the evidence from our domestic animals of many kinds which have run wild in several parts of the world: if the statements of the rate of increase of slow-breeding cattle and horses in South America, and latterly in Australia, had not been well authenticated, they would have been quite incredible. So it is with plants: cases could be given of introduced plants which have become common throughout whole islands in a period of less than ten years, Several of the plants now most numerous over the wide plains of La Plata, clothing square leagues of surface almost to the exclusion of all other plants, have been introduced from Europe; and there are plants which now range in India, as I hear from Dr Falconer, from Cape Comorin to the Himalaya, which have been imported from America since its discovery. In such cases, and endless instances could be given, no one supposes that the fertility of these animals or plants has been suddenly and temporarily increased in any sensible degree. The obvious explanation is that the conditions of life have been very favourable, and that there has consequently been less destruction of the old and young, and that nearly all the young have been enabled to breed. In such cases the geometrical ratio of increase, the result of which never fails to be surprising, simply explains the extraordinarily rapid increase and wide diffusion of naturalised productions in their new homes.

31. In a state of nature almost every plant produces seed, and amongst animals there are very few which do not annually pair. Hence we may confidently assert, that all plants and animals are tending to increase at a geometrical ratio, that all would most rapidly stock every station in which they could any how exist, and that the geometrical tendency to increase must be checked by destruction at some period of life. Our familiarity with the larger domestic animals tends, I think, to mislead us: we see no great destruction falling on them, and we forget that thousands are annually slaughtered for food, and that in a state of nature an equal number would have somehow to be disposed of.

32. The only difference between organisms which annually produce eggs or seeds by the thousand, and those which produce extremely few, is, that the slow-breeders would require a few more years to people, under favourable conditions, a whole district, let it be ever so large. The condor lays a couple of eggs and the ostrich a score, and yet in the same country the condor may be the more numerous of the two: the Fulmar petrel lays but one egg, yet it is believed to be the most numerous bird in the world. One fly deposits hundreds of eggs, and another, like the hippobosca, a single one; but this difference does not determine how many individuals of the two species can be supported in a district. A large number of eggs is of some importance to those species, which depend on a rapidly fluctuating amount of food, for it allows them rapidly to increase in number. But the real importance of a large number of eggs or seeds is to make up for much destruction at some period of life; and this period in the great majority of cases is an early one. If an animal can in any way protect its own eggs or young, a small number may be produced, and yet the average stock be fully kept up; but if many eggs or young are destroyed, many must be produced, or the species will become extinct. It would suffice to keep up the full number of a tree, which lived on an average for a thousand years, if a single seed were produced once in a thousand years, supposing that this seed were never destroyed, and could be ensured to germinate in a fitting place. So that in all cases, the average number of any animal or plant depends only indirectly on the number of its eggs or seeds.

33. In looking at Nature, it is most necessary to keep the foregoing considerations always in mind never to forget that every single organic being around us may be said to be striving to the utmost to increase in numbers; that each lives by a struggle at some period of its life; that heavy destruction inevitably falls either on the young or old, during each generation or at recurrent intervals. Lighten any check, mitigate the destruction ever so little, and the number of the species will almost instantaneously increase to any amount. The face of Nature may be compared to a yielding surface, with ten thousand sharp wedges packed close together and driven inwards by incessant blows, sometimes one wedge being struck, and then another with greater force.

34. What checks the natural tendency of each species to increase in number is most obscure. Look at the most vigorous species; by as much as it swarms in numbers, by so much will its tendency to increase be still further increased. We know not exactly what the checks are in even one single instance. Nor will this surprise any one who reflects how ignorant we are on this head, even in regard to mankind, so incomparably better known than any other animal. This subject has been ably treated by several authors, and I shall, in my future work, discuss some of the checks at considerable length, more especially in regard to the feral animals of South America. Here I will make only a few remarks, just to recall to the reader's mind some of the chief points. Eggs or very young animals seem generally to suffer most, but this is not invariably the case. With plants there is a vast destruction of seeds, but, from some observations which I have made, I believe that it is the seedlings which suffer most from germinating in ground already thickly stocked with other plants. Seedlings, also, are destroyed in vast numbers by various

enemies; for instance, on a piece of ground three feet long and two wide, dug and cleared, and where there could be no choking from other plants, I marked all the seedlings of our native weeds as they came up, and out of the 357 no less than 295 were destroyed, chiefly by slugs and insects. If turf which has long been mown, and the case would be the same with turf closely browsed by quadrupeds, be let to grow, the more vigorous plants gradually kill the less vigorous, though fully grown, plants: thus out of twenty species growing on a little plot of turf (three feet by four) nine species perished from the other species being allowed to grow up freely.

35. The amount of food for each species of course gives the extreme limit to which each can increase; but very frequently it is not the obtaining food, but the serving as prey to other animals, which determines the average numbers of a species. Thus, there seems to be little doubt that the stock of partridges, grouse, and hares on any large estate depends chiefly on the destruction of vermin. If not one head of game were shot during the next twenty years in England, and, at the same time, if no vermin were destroyed, there would, in all probability, be less game than at present, although hundreds of thousands of game animals are now annually killed. On the other hand, in some cases, as with the elephant and rhinoceros, none are destroyed by beasts of prey: even the tiger in India most rarely dares to attack a young elephant protected by its dam.

36. Climate plays an important part in determining the average numbers of a species, and periodical seasons of extreme cold or drought, I believe to be the most effective of all checks. I estimated that the winter of 1854-55 destroyed four-fifths of the birds in my own grounds; and this is a tremendous destruction, when we remember that ten per cent. is an extraordinarily severe mortality from epidemics with man. The action of climate seems at first sight to be quite independent of the struggle for existence; but in so far as climate chiefly acts in reducing food, it brings on the most severe struggle between the individuals, whether of the same or of distinct species, which subsist on the same kind of food. Even when climate, for instance extreme cold, acts directly, it will be the least vigorous, or those which have got least food through the advancing winter, which will suffer most. When we travel from south to north, or from a damp region to a dry, we invariably see some species gradually getting rarer and rarer, and finally disappearing; and the change of climate being conspicuous, we are tempted to attribute the whole effect to its direct action. But this is a very false view: we forget that each species, even where it most abounds, is constantly suffering enormous destruction at some period of its life, from enemies or from competitors for the same place and food; and if these enemies or competitors be in the least degree favoured by any slight change of climate, they will increase in numbers, and, as each area is already fully stocked with inhabitants, the other species will decrease. When we travel southward and see a species decreasing in numbers, we may feel sure that the cause lies quite as much in other species being favoured, as in this one being hurt. So it is when we travel northward, but in a somewhat lesser degree, for the number of species 204
of all kinds, and therefore of competitors, decreases northwards; hence in going northward, or in ascending a mountain, we far oftener meet with stunted forms, due to the *directly* injurious action of climate, than we do in proceeding southwards or in descending a mountain. When we reach the Arctic regions, or snow-capped summits, or absolute deserts, the struggle for life is almost exclusively with the elements.

37. That climate acts in main part indirectly by favouring other species, we may clearly see in the prodigious number of plants in our gardens which can perfectly well endure our climate, but which never become naturalised, for they cannot compete with our native plants, nor resist destruction by our native animals.

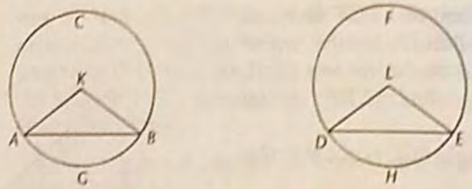
38. When a species, owing to highly favourable circumstances, increases inordinately in numbers in a small tract, epidemics at least, this seems generally to occur with our game animals often ensue: and here we have a limiting check independent of the struggle for life. But even some of these so-called epidemics appear to be due to parasitic worms, which have from some cause, possibly in part through facility of diffusion amongst the crowded animals, been disproportionably favoured: and here comes in a sort of struggle between the parasite and its prey.

39. On the other hand, in many cases, a large stock of individuals of the same species, relatively to the numbers of its enemies, is absolutely necessary for its preservation. Thus we can easily raise plenty of corn and rape-seed, &c., in our fields, because the seeds are in great excess compared with the number of birds which feed on them; nor can the birds, though having a superabundance of food at this one season, increase in number proportionally to the supply of seed, as their numbers are checked during winter: but any one who has tried, knows how troublesome it is to get seed from a few wheat or other such plants in a garden; I have in this case lost every single seed. This view of the necessity of a large stock of the same species for its preservation, explains, I believe, some singular facts in nature, such as that of very rare plants being sometimes extremely abundant in the few spots where they do occur; and that of some social plants being social, that is, abounding in individuals, even on the extreme confines of their range. For in such cases, we may believe, that a plant could exist only where the conditions of its life were so favourable that many could exist together, and thus save each other from utter destruction. I should add that the good effects of frequent intercrossing, and the ill effects of close interbreeding, probably come into play in some of these cases; but on this intricate subject I will not here enlarge.

40. Many cases are on record showing how complex and unexpected are the checks and relations between organic beings, which have to struggle together in the same country. I will give only a single instance, which, though a simple one, has interested me. In Staffordshire, on the estate of a relation where I had ample means of investigation, there was a large and extremely barren heath, which had never been touched by the hand of man; but several hundred acres of exactly the same nature had been enclosed twenty-five years previously and planted with Scotch fir. The change in the native vegetation of the planted part of the heath was most remarkable, more than is generally seen in passing from one quite different soil to another: not only the proportional numbers of the heath-plants were wholly changed, but twelve species of plants (not counting grasses and carices) flourished in the plantations, which could not be found on the heath. The effect on the insects must have been still greater, for six insectivorous birds were very common in the plantations, which were not to be seen on the heath; and the heath was frequented by two or three distinct insectivorous birds. Here we see how potent has been the effect of the introduction of a single tree, nothing whatever else having been done, with the exception that the land had been enclosed, so that cattle could not enter. But how important an element enclosure is, I plainly saw near Farnham, in Surrey. Here there are extensive heaths, with a few clumps of old Scotch firs on the distant hill-tops: within the last ten years large spaces have been enclosed, and self-sown firs are now springing up in multitudes, so close together that all cannot live. When I ascertained that these young trees had not been sown or planted, I was so much surprised at their numbers that I went to several points of view, whence I could examine hundreds of acres of the unenclosed heath, and literally I could not see a single Scotch fir, except the old planted clumps. But on looking closely between the stems of the heath, I found a multitude of seedlings and little trees, which had been perpetually browsed down by the cattle. In one square yard, at a point some hundreds yards distant from one of the old clumps, I counted thirty-two little trees; and one of them, judging from the rings of growth, had during twenty-six years tried to raise its head above the stems of the heath, and had failed. No wonder that, as soon as the land was enclosed, it became thickly clothed with vigorously growing young firs. Yet the heath was so extremely barren and so extensive that no one would ever have imagined that cattle would have so closely and effectually searched it for food.

44. Here we see that cattle absolutely determine the existence of the Scotch fir; but in several parts of the world insects determine the existence of cattle. Perhaps Paraguay offers the most curious instance of this; for here neither cattle nor horses nor dogs have ever run wild, though they swarm southward and northward in a feral state; and Azara and Rengger have shown that this is caused by the greater number in Paraguay of a certain fly, which lays its eggs in the navels of these animals when first born. The increase of these flies, numerous as they are, must be habitually checked by some means, probably by birds. Hence, if certain insectivorous birds (whose numbers are probably regulated by hawks or beasts of prey) were to increase in Paraguay, the flies would decrease then cattle and horses would become feral, and this would certainly greatly alter (as indeed I have observed in parts of South America) the vegetation: this again would largely affect the insects; and this, as we just have seen in Staffordshire, the insectivorous birds, and so onwards in ever-increasing circles of complexity. We began this series by insectivorous birds, and we have ended with them. Not that in nature the relations can ever be as simple as this. Battle within battle must ever be recurring with varying success; and yet in the long-run the forces are so nicely balanced, that the face of nature remains uniform for long periods of time, though assuredly the merest trifle would often give the victory to one organic being over another. Nevertheless so profound is our ignorance, and so high our presumption, that we marvel when we hear of the extinction of an organic being; and as we do not see the cause, we invoke cataclysms to desolate the world, or invent laws on the duration of the forms of life!

45. I am tempted to give one more instance showing how plants and animals, most remote in the scale of nature, are bound together by a web of complex relations. I shall hereafter have occasion to show that the exotic Lobelia fulgens, in this part of England, is never visited by insects, and consequently, from its peculiar structure, never can set a seed. Many of our orchidaceous plants absolutely require the visits of moths to remove their pollen-masses and thus to fertilise them. I have, also, reason to believe that humble-bees are indispensable to the fertilisation of the heartsease (Viola tricolor), for other bees do not visit this flower. From experiments which I have tried, I have found that the visits of bees, if not indispensable, are at least highly beneficial to the fertilisation of our clovers; but humble-bees alone visit the common red clover (Trifolium pratense), as other bees cannot reach the nectar. Hence I have very little doubt, that if the whole genus of humble-bees became extinct or very rare in England, the heartsease and red clover would become very rare, or wholly disappear. The number of humble-bees in any district depends in a great degree on the number of field-mice, which destroy their combs and nests; and Mr H. Newman, who has long attended to the habits of humble-bees, believes that 'more than two thirds of them are thus destroyed all over England.' Now the number of mice is largely dependent, as every one knows, on the number of cats; and Mr Newman says, 'Near villages and small towns I have found the nests of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice.' Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!



therefore the two sides *AK*, *KB* are equal to the two sides *DL*, *LE*;
and the base *AB* is equal to the base *DE*;
therefore the angle *AKB* is equal to the angle *DLE*. [I. 8]

But equal angles stand on equal circumferences, when they are at the centres; [III. 26]
therefore the circumference *AGB* is equal to *DHE*.

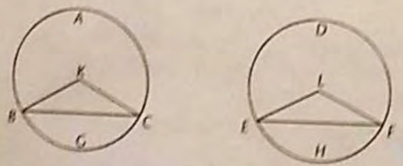
And the whole circle *ABC* is equal to the whole circle *DEF*;
therefore the circumference *ACB* which remains is also equal to the circumference *DFE* which remains.

Therefore etc.

Q.E.D.

Proposition 29

In equal circles equal circumferences are subtended by equal straight lines.



Let *ABC*, *DEF* be equal circles, and in them let equal circumferences *BGC*, *EHF* be cut off; and let the straight lines *BC*, *EF* be joined;
I say that *BC* is equal to *EF*.

For let the centres of the circles be taken, and let them be *K*, *L*; let *BK*, *KC*, *EL*, *LF* be joined.

Now, since the circumference *BGC* is equal to the circumference *EHF*,
the angle *BKC* is also equal to the angle *ELF*. [III. 27]

And, since the circles *ABC*, *DEF* are equal,
the radii are also equal;
therefore the two sides *BK*, *KC* are equal to the two sides *EL*, *LF*;
and they contain equal angles;
therefore the base *BC* is equal to the base *EF*. [I. 4]

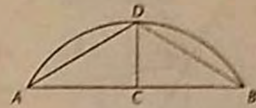
Therefore etc.

Q.E.D.

Proposition 30

To bisect a given circumference.

Let *ADB* be the given circumference;
thus it is required to bisect the circumference *ADB*.



Let *AB* be joined and bisected at *C*; from the point *C* let *CD* be drawn at right angles to the straight line *AB*, and let *AD*, *DB* be joined.

Then, since *AC* is equal to *CB*, and *CD* is common,
the two sides *AC*, *CD* are equal to the two sides *BC*, *CD*;
and the angle *ACD* is equal to the angle *BCD*, for each is right;
therefore the base *AD* is equal to the base *DB*. [I. 4]

But equal straight lines cut off equal circumferences, the greater equal to the greater, and the less to the less; [III. 28]
and each of the circumferences *AD*, *DB* is less than a semicircle;
therefore the circumference *AD* is equal to the circumference *DB*.

Therefore the given circumference has been bisected at the point *D*.

Q.E.F.

Proposition 31

In a circle the angle in the semicircle is right, that in a greater segment less than a right angle, and that in a less segment greater than a right angle; and further the angle of the greater segment is greater than a right angle, and the angle of the less segment less than a right angle.

Let *ABCD* be a circle, let *BC* be its diameter, and *E* its centre, and let *BA*, *AC*, *AD*, *DC* be joined;
I say that the angle *BAC* in the semicircle *BAC* is right,
the angle *ABC* in the segment *ABC* greater than the semicircle is less than a right angle,
and the angle *ADC* in the segment *ADC* less than the semicircle is greater than a right angle.

Let *AE* be joined, and let *BA* be carried through to *F*.

Then, since *BE* is equal to *EA*,
the angle *ABE* is also equal to the angle *BAE*. [I. 5]

Again, since *CE* is equal to *EA*,
the angle *ACE* is also equal to the angle *CAE*. [I. 5]

Therefore the whole angle *BAC* is equal to the two angles *ABC*, *ACB*.

But the angle *FAC* exterior to the triangle *ABC* is also equal to the two angles *ABC*, *ACB*; [I. 32]
therefore the angle *BAC* is also equal to the angle *FAC*;
therefore each is right; [I. Def. 10]
therefore the angle *BAC* in the semicircle *BAC* is right.

Next, since in the triangle *ABC* the two angles *ABC*, *BAC* are less than two right angles, [I. 17]
and the angle *BAC* is a right angle,
the angle *ABC* is less than a right angle;

and it is the angle in the segment ABC greater than the semicircle.

Next, since $ABCD$ is a quadrilateral in a circle, and the opposite angles of quadrilaterals in circles are equal to two right angles, [III. 22]
while the angle ABC is less than a right angle,
therefore the angle ADC which remains is greater than a right angle;
and it is the angle in the segment ADC less than the semicircle.

I say further that the angle of the greater segment, namely that contained by the circumference ABC and the straight line AC, is greater than a right angle;
and the angle of the less segment, namely that contained by the circumference ADC and the straight line AC, is less than a right angle.

This is at once manifest.

For, since the angle contained by the straight lines BA, AC is right,
the angle contained by the circumference ABC and the straight line AC is greater than a right angle.

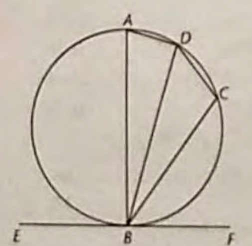
Again, since the angle contained by the straight lines AC, AF is right,
the angle contained by the straight line CA and the circumference ADC is less than a right angle.

Therefore etc.

Q.E.D.

Proposition 32

If a straight line touch a circle, and from the point of contact there be drawn across, in the circle, a straight line cutting the circle, the angles which it makes with the tangent will be equal to the angles in the alternate segments of the circle.



For let a straight line EF touch the circle $ABCD$ at the point B, and from the point B let there be drawn across, in the circle $ABCD$, a straight line BD cutting it;
I say that the angles which BD makes with the tangent EF will be equal to the angles in the alternate segments of the circle, that is, that the angle FBD is equal to the angle constructed in the segment BAD, and the angle EBD is equal to the angle constructed in the segment DCB.

For let BA be drawn from B at right angles to EF,
let a point C be taken at random on the circumference BD,
and let AD, DC, CB be joined.

Then, since a straight line EF touches the circle $ABCD$ at B,

and BA has been drawn from the point of contact at right angles to the tangent,
the centre of the circle $ABCD$ is on BA. [III. 19]

Therefore BA is a diameter of the circle $ABCD$;
therefore the angle ADB, being an angle in a semicircle, is right. [III. 31]

Therefore the remaining angles BAD, ABD are equal to one right angle. [I. 32]

But the angle ABF is also right;
therefore the angle ABF is equal to the angles BAD, ABD.

Let the angle ABD be subtracted from each;
therefore the angle DBF which remains is equal to the angle BAD in the alternate segment of the circle.

Next, since $ABCD$ is a quadrilateral in a circle,
its opposite angles are equal to two right angles. [III. 22]

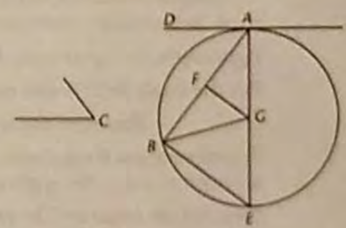
But the angles DBF, DBE are also equal to two right angles;
therefore the angles DBF, DBE are equal to the angles BAD, BCD,
of which the angle BAD was proved equal to the angle DBF;
therefore the angle DBE which remains is equal to the angle DCB in the alternate segment DCB of the circle.

Therefore etc.

Q.E.D.

Proposition 33

On a given straight line to describe a segment of a circle admitting an angle equal to a given rectilineal angle.



Let AB be the given straight line, and the angle at C the given rectilineal angle;
thus it is required to describe on the given straight line AB a segment of a circle admitting an angle equal to the angle at C.

The angle at C is then acute, or right, or obtuse.

First, let it be acute, and, as in the first figure, on the straight line AB, and at the point A, let the angle BAD be constructed equal to the angle at C;
therefore the angle BAD is also acute.

Let AE be drawn at right angles to DA, let AB be bisected at F, let FG be drawn from the point F at right angles to AB, and let GB be joined.

Then, since AF is equal to FB,
and FG is common,
the two sides AF, FG are equal to the two sides BF, FG;
and the angle AFG is equal to the angle BFG;
therefore the base AG is equal to the base BG. [I. 4]

Therefore the circle described with centre G and distance GA will pass through B also.

26 The Second World War

1933–1945

***Raising the Flag on Iwo Jima* (February 23, 1945)** Five members of the United States Marine Corps raise the U.S. flag on Mount Suribachi, during the Battle of Iwo Jima. Three of these Marines would die within days after this photograph was taken. The image earned photographer Joe Rosenthal the Pulitzer Prize. A bronze statue of this scene is the centerpiece of the Marine Corps War Memorial in Virginia.

When Franklin Roosevelt became president in 1933, he shared with most Americans a determination to stay out of international disputes. His focus was on combating the Great Depression at home. While the United States had become deeply involved in global trade during the twenties, it had remained aloof from global conflicts. So-called isolationists insisted that there was no justification for America to become embroiled in international affairs, much less another major war. With each passing year during the thirties, however, Germany, Italy, and Japan threatened the peace and stability of Europe and Asia.

Roosevelt strove mightily to keep the United States out of what he called the "spreading epidemic of world lawlessness," as fascist dictatorships in Germany and Italy and ultranationalist militarists in Japan violated international law by invading neighboring countries. By the end of the decade, Roosevelt had decided that the only way for the United States to avoid fighting in another war was to offer all possible assistance to its allies, Great Britain, France, and China.

Roosevelt's efforts to stop "aggressor nations" ignited a fierce debate between isolationists and interventionists which ended with shocking suddenness on December 7, 1941, when Japan staged a surprise attack against U.S. military bases at Pearl Harbor in Hawaii. The second world war that Americans had struggled to avoid had arrived at last. It would become the most significant event of the twentieth century, engulfing five continents and leaving few people untouched.

The Japanese attack unified Americans as never before. Men and women rushed to join the armed forces. Eventually, 16.4 million people would serve

focus questions

1. How did German and Japanese actions lead to the outbreak of war in Europe and Asia?
2. How did President Roosevelt and Congress respond to the outbreak of wars in Europe and Asia between 1933 and 1941?
3. What were the effects of the Second World War on American society?
4. What were the major factors that enabled the United States and its allies to win the war in Europe?
5. How were the Japanese defeated in the war in the Pacific?
6. How did President Roosevelt and the Allies work to shape the postwar world?