

73.26°, and on the diagram (Fig. 1945) is represented by the position of the line  $Mx_0$ . The mean of any character may be taken also as the *type* for the species, and this is used much more frequently than the mode as the standard from which to measure variations. We may obtain a rough idea of the variability of a character by observing the extreme *range* of variation from the lowest to the highest value. But this cannot be done very accurately and conveys no information as to the relative frequency of the intermediate values. A better idea may be obtained by calculating what is called the *standard deviation*

( $\sigma = \sqrt{\frac{\sum(x^2f)}{n}}$ , see article *Variation*). In our example this has the value of 4.36°, and is represented at  $\sigma$  in the diagram. Knowing the total number of individuals measured, the mean, and the standard deviation, it is possible by the use of appropriate formulæ and tables (Davenport, "Statistical Methods") to calculate and plot the corresponding theoretical *normal curve* of chance. This is represented in the diagram by the heavy broken line. This means that if, instead of taking ninety-seven individuals and dividing them into five classes, we had taken a very large number of individuals, several thousand at least, and divided them into very many classes, we should expect to obtain a series of rectangles, the tops of which would follow the broken line; and in our diagram it will be noticed that the straight lines connecting the middle points in the tops of the rectangles follow pretty closely the theoretical curve. Thus, although only ninety-seven specimens were taken, much too few for accurate results, it is evident that the different variations in the acuteness of the apex in *Purpura* occur approximately with the frequency predicted by the law of chance. In calculating this curve it has been assumed that the mode and the mean coincide and that variations less than the mean and those greater than the mean occur normally with equal frequency, so that the curve is perfectly symmetrical. In many cases, however, it has been found that the frequency of variations is best represented by a curve where the mean and the mode do not coincide. In such cases the curve is asymmetrical, and is called a *skew curve*.

In other cases it has been found that there are two or more classes containing a large number of individuals with intermediate classes containing few. The curve plotted from such a series of observations would present two or more modes, as the case might be, and would be what is called a *multimodal curve*. An example of such

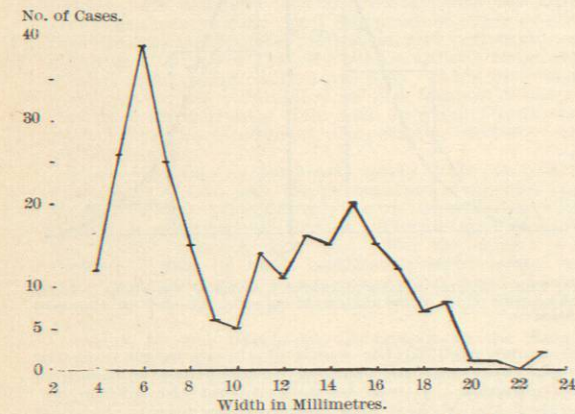


FIG. 1946.—Example of a Multimodal Curve. Variation in the width of the leaf of the cat-tail, *Typha latifolia* and *T. angustifolia*. (After Blankinship.)

a curve is shown in Fig. 1946, which represents the distribution of variations in the width of the leaf of the cat-tail. The data from which the curve is plotted are ob-

tained from measurements of the widest part of the widest leaf in two hundred and fifty specimens, and are as follows:

CLASSES.					
Width in millimetres.	Number of cases.	Width in millimetres.	Number of cases.	Width in millimetres.	Number of cases.
4	12	11	14	18	7
5	26	12	11	19	9
6	39	13	16	20	11
7	25	14	15	21	11
8	15	15	20	22	0
9	6	16	15	23	0
10	5	17	12		

After allowing for minor irregularities, due probably to the small number of observations, there are evidently two modes, one at 6 mm. and the other at 15.

This illustrates the distinction between *individual variation* and *racial variation*. So long as the variations are distributed about a single type we have what is called individual variation, and the variability of the species in respect to the character in question is measured by its standard deviation. But where there are several modes—several types about which variations are distributed—we have what may be called racial variation, and this kind of variability is measured by the number of modes and their distance apart. Racial variability tends to divide the species into races, or sub-species. In fact, botanists divide the cat-tails into two distinct species, *Typha latifolia* L. and *T. angustifolia* L. But Blankinship has shown that these two groups grade into one another in all their characters, and this is a good example of the difficulty, often met with, of drawing a sharp line between species.

So far single variations have been treated as if they were isolated objects. As a matter of fact, they never occur as such in nature, for every individual is made up of a great many characters; and the question arises, Is there any relation between the deviation of one character and the deviations of other characters in the same individual? Such a relation is called the *correlation of variations*, and Darwin gave many interesting examples of it. Since then Galton has pointed out a method by which correlation may be studied very exactly, and the degree of correlation may be given mathematical expression. If in a number of individuals character *A* deviates from its mean *Ma* by the amount *Xa*, it is possible to determine what will be the average deviation *Xb* of the character *B* from its mean *Mb* (see article *Variation*).

While much work is still to be done in this line, enough has been accomplished to show that correlations of this kind are common among normal variations; and this is a fact of the highest importance for the theory of evolution.

**Heredity.**—Heredity is a special case of correlation. It is the correlation between the variations of homologous organs in individuals related by birth, especially those in the relation of parent and offspring. The facts of heredity are of equal importance with the facts of variation. For if this correlation did not exist, or, to use the common metaphor, if there were no inheritance of variations, progressive change of type, evolution, would be as impossible as if there were no variation at all.

The facts and theories of inheritance will be discussed more fully elsewhere (see articles *Heredity* and *Reversion*). Attention here will be confined to a few facts of especial importance in connection with the subject of the present article.

In the first place it may be noted that there are three chief forms of inheritance: (1) *Blended inheritance* where the character in the offspring partakes of the qualities of both parents, as in stature; (2) *exclusive inheritance*, where the character in the child is like that in one parent, but not like the other, if it differ from the first, as in the color of the eye; (3) *particulate inheritance*, where the

child resembles one parent in one character and the other in another character. For example, a child may have its mother's eyes and its father's nose.

In general, all congenital characters, whether they be new acquisitions or inheritances, may be transmitted to the offspring. But it is extremely doubtful if acquired modifications are ever inherited (see p. 35). Sometimes the correlation of the offspring will be much stronger with one parent than with the other, and the parent which the offspring tends to resemble the most is then said to be *prepotent*. This is often the case with sports, as in the famous Ancon breed of sheep that arose in Massachusetts in the latter part of the eighteenth century. In domestic races pure bred animals are generally prepotent over mongrels.

Heredity is measured in the same way that correlation is. But a complication arises owing to the fact that most individuals have two parents. In order to avoid the difficulty of measuring the correlation of three variables, the two parents are combined into one imaginary individual known as the *mid-parent*. Then it is easy to find the correlation between mid-parent and offspring.

Pearson gives the following formula for finding the mid-parent:

$$\frac{1}{2}(h_1 + \frac{\sigma_1}{\sigma_2} h_2) = H$$

where  $h_1$  = value of the character in the father,  $h_2$  = the same in mother,  $\sigma_1$  = standard deviation of fathers in general,  $\sigma_2$  = the same for mothers, and  $H$  = the character in the mid-parent.

It might be expected that the average offspring would be like the mid-parent. But, as a matter of fact, it is found by observation that, while some children may be exactly like the mid-parent and some more peculiar, the average of the offspring will be less peculiar, more nearly like the general average of the population, than the mid-parent, if that be possible. This is called *regression*. The amount of regression differs with different characters in different species, but in general it may be said that the offspring on the average will be about two-thirds as peculiar as the mid-parent, or one-third as either parent considered alone. This may be accounted for, perhaps, by reference to the previous ancestry. For if there be no selection or inbreeding, the number of ancestors in each generation increase as we go backward in geometrical ratio until they soon form all together a fair sample of the population as a whole. In the tenth generation back there are ten hundred and twenty-four ancestors.

On the other hand, we have the seemingly paradoxical fact of regression in the opposite sense. That is, if we take a large number of children all deviating in a certain character to a given degree from the average of the population, it will be found that the average of their mid-parents will be only one-third as peculiar. This is simply due to the fact that mediocre mid-parents are more common than peculiar ones (see Fig. 1945). From these facts Galton has derived a law of heredity, which Pearson states in the following words:

"Each parent contributes on an average one-quarter, or  $(\frac{1}{2})^2$ , each grandparent one-sixteenth, or  $(\frac{1}{2})^4$ , and so on, and that generally the occupier of each ancestral place in the *n*th degree, whatever the value of *n*, contributes  $(\frac{1}{2})^{2n}$  of the heritage."

Mathematically this would be,

$$h = \frac{1}{4} H_1 + \frac{1}{4} H_2 + \frac{1}{16} H_3 + \dots \text{etc.},$$

a geometrical progression approaching a limit = 1, when  $h$  = the average deviation of the offspring, and  $H_1, H_2, H_3$ , etc., = the deviation in the mid-parent, mid-grandparent, mid-great-grandparent, etc. But Galton's series,  $\frac{1}{4}, \frac{1}{16}, \dots$ , etc., may not be true in all cases. So Pearson replaces these figures by symbols that may express any geometrical progression,  $\gamma a, \gamma a^2, \gamma a^3, \dots, \gamma a^{10}$ , etc., in which there are two factors, one constant in each generation,  $\gamma$ , and one which varies in geometrical

series,  $a, a^2, a^3$ , etc.\* Then allowing for difference of variability, as well as differences in deviation and mean, of past generations of mid-parents, Pearson gets the following *law of ancestral heredity*:

$$h = \gamma \left\{ \frac{1}{1+\gamma} \frac{\sigma_1}{\sigma_1} H_1 + \frac{1}{(1+\gamma)^2} \frac{\sigma_2}{\sigma_2} H_2 + \dots \frac{1}{(1+\gamma)^{10}} \frac{\sigma_{10}}{\sigma_{10}} H_{10} + \dots \text{etc.} \right\}$$

where  $h$  = average deviation of the offspring,  $H_1, H_2, H_3$ , etc., = the deviation from the means of their generation of the mid-parents, mid-grandparents, etc.,  $\sigma =$  standard deviation, variability, of all offspring,  $\sigma_1, \sigma_2, \sigma_3$ , etc., = variability of the race in the generations to which the successive mid-parents belong, and  $\gamma$  is the *constant of heredity*, upon which all hereditary influence depends. This, in Mr. Galton's formula, would be  $\gamma = 1$ . But it may be found to vary in different species and in different organs.

As to the importance of the law of ancestral heredity, Pearson says: "If Darwinism be the true view of evolution, *i.e.*, if we are to describe evolution by natural selection combined with heredity, then the law which gives us definitely and concisely the type of the offspring in terms of ancestral peculiarities is at once the foundation stone of biology and the basis upon which heredity becomes an exact branch of science."

**The Struggle for Existence.**—With the struggle for existence we come to the first of the distinctively Darwinian factors of evolution.

Darwin's definition is as follows. He says: "I should premise that I use this term in a large and metaphorical sense, including dependence of one being on another, and including 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, though more properly it should be said to be dependent on the moisture. A plant which annually produces a thousand seeds, of which only one of an average 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 mistletoe 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 languishes and dies. But several seedling mistletoes growing close together on the same branch may more truly be said to struggle with each other. As the mistletoe is disseminated by birds, its existence depends on them; and it may metaphorically be said to struggle with other fruit-bearing plants, in tempting the birds to devour and thus disseminate its seeds. In these several senses, which pass into each other, I use for convenience's sake the general term struggle for existence" ("Origin of Species," 6th ed. vol. i., p. 78).

Wallace uses the term without giving a definition. In his essay of 1858 he says: "The life of wild animals is a struggle for existence. The full exertion of all their faculties and all their energies is required to preserve their own existence and provide for that of their infant offspring. The possibility of procuring food during the least favorable seasons, and of escaping the attacks of their most dangerous enemies, are the primary conditions, which determine the existence both of individuals and of entire species."

\* Then substituting, we have:

$$h = \gamma (a H_1 + a^2 H_2 + a^3 H_3 + \dots \text{etc.}).$$

Now when  $\gamma (a + a^2 + a^3 + \dots \text{etc.}) = 1$ , then  $\frac{\gamma a}{1-a} = 1$

$$\therefore \gamma = \frac{1-a}{a} = \frac{1}{a} - 1. \dots \frac{1}{a} = 1 + \gamma, \text{ and } a = \frac{1}{1+\gamma}.$$

So  $a, a^2, a^3, \dots, a^{10}, \dots$ , etc., may be replaced in the formula by  $\frac{1}{1+\gamma}, \frac{1}{(1+\gamma)^2}, \dots, \frac{1}{(1+\gamma)^{10}}, \dots$ , etc.

This term, struggle for existence, is a convenient one, and it conveys a very vivid impression as to what takes place. But it may convey a false idea unless we are careful to bear in mind the metaphorical character of the expression. It may help us to do this if we can find for this term a definition which in itself shall be free from metaphors.

Spencer has defined life as "the continuous adjustment of internal relations to external relations" ("Principles of Biology," 2d ed., vol. i., p. 99). So long as the external relations are favorable, this adjustment is made easily. When they become unfavorable it is made with difficulty, and when it becomes impossible the organism dies. Therefore we may define the struggle for existence as the tendency of organisms to preserve a continuous adjustment of internal relations to unfavorable external relations.

The meaning of this will be more clear when we consider what are these unfavorable external relations in which life becomes a struggle for existence. They may be classified under three divisions: (1) adverse physical conditions, (2) enemies, and (3) competition.

1. *The Struggle against Adverse Physical Conditions.*—Conditions that are adverse for one species may be favorable for another. Thus the polar bear is unable to live on the hot sands of the Sahara, and the polar ice fields would be equally fatal to the lion. A fish cannot live in the air, nor a bird under water. So what constitutes an unfavorable physical condition depends largely upon the constitution of the organism that meets it.

There are doubtless large numbers of individuals and species which, so long as they remain in their native habitat, never have to contend with adverse physical conditions. Such is true, for example, of the majority of dwellers in the sea, and it applies equally well to the inhabitants of many tropical lands. The islands of the Antilles with their abundant rains, and even, warm temperature, are as favorable as possible for life. The only unfavorable condition is the occasional hurricane, when the rivers "come down," as they say, in irresistible torrents and the wind tears huge trees up by the roots, while the seas dash against the shores with appalling fury. Except for these infrequent catastrophes, the processes of life are favored continually by the physical conditions on land as well as in the sea.

It is in our own temperate region, with its extremes of heat and cold and sudden changes from moisture to dryness, that the adjustment of internal relations to external relations is attended with difficulty. We see this adjustment taking place annually at the time of the falling of the leaf, when the trees prepare themselves to withstand the frosts of winter. The leaves are cut off by an ingrowth of bark. The absorption of water is suspended, and the protoplasm becomes concentrated in the cells already heavily laden with starch. The embryonic tissue is confined to a thin layer under the bark and to small areas in the buds protected by thick envelopes, often lined with down, and varnished on the outside; and the cells of other parts acquire a thick wall of cellulose which renders them incapable of further growth. Thus in the cool days of fall the trees prepare to resist the freezing of winter, and usually this is successful. But sometimes it fails.

The summer of 1879 in England was cool and damp so that the new wood was not properly matured. This was followed by an unusually severe winter, and all over the country thousands of perennial plants were killed or severely injured by freezing. In one locality every common shrub was killed to the ground (Henslow, "Frost Report," 1887). In this country it happens frequently that warm days in early spring tempt the trees to throw off their winter protection, and send forth the young shoots and flower-buds. Then comes a late frost, and all the growing parts are killed.

But extreme cold is even more disastrous to animals. Darwin says: "I estimated (chiefly from the greatly reduced numbers of nests in the spring) that the winter of 1854-55 destroyed four-fifths of the birds in my own

grounds." After the great storm of February 1st, 1898, Professor Bumpus found one hundred and thirty-six sparrows lying helpless upon the ground in Providence, of which sixty-four were dead or dying.

The effects of drought upon animals as well as plants are so well known that they need not be described.

2. *Enemies.*—Darwin regards extremes of cold and drought as probably the most effective of all checks on population. But the depredations of enemies constitute a check which is even of more universal effect.

Ernest Seton Thompson says: "The life of a wild animal *always has a tragic end.*" There is hardly an animal or a plant, from the humblest protophyte to man himself, that is not subject to the attacks of other organisms. Herbivorous animals feed upon the plants, and these animals in their turn form the food of carnivorous species. Those that escape being devoured in this way, and successfully resist the effects of climate usually at last fall a prey to the inroads of bacteria or other parasites.

Plants are particularly subject to destruction in the early stages of their growth. Darwin dug and cleared a piece of ground three feet long and two feet wide, and then marked all the seedlings of the native weeds as they came up, and out of the 357 no less than 295 were destroyed, chiefly by slugs and insects ("Origin of Species," vol. i., p. 83).

Judd says: "It is not at all uncommon for a crow or blackbird to eat from 30 to 50 seeds of smartweed or bindweed, or a field sparrow 100 seeds of crab grass, at a single meal. In the stomach of Nuttall's sparrow were found 300 seeds of amaranth, and in another 300 seeds of lamb's quarters, a tree sparrow had consumed 700 seeds of pigeon grass, while a snowflake from Shrewsbury, Mass., which had been breakfasting in a garden in February, had picked up 1,000 seeds of pigweed" ("Year Book, United States Agricultural Department," 1898, p. 222). Professor Beal has estimated that in the State of Iowa the tree sparrows alone destroy annually about 1,750,000 pounds, or 875 tons of weed seeds (*l.c.*, p. 226).

These seed-eating birds are in turn preyed upon by the various hawks and owls.

In the sea, plants form the food of few species except the most minute animals. A vast majority of marine species are carnivorous, and the destruction is enormous. Brooks gives a vivid picture of this struggle ("Foundations of Zoology," pp. 220-224 and 231-233). Speaking of the inlets among coral islands he says, "Nothing could illustrate the fierceness of the struggle for food among the animals on a crowded sea-bottom more vividly than the emptiness of the water in coral sounds where the bottom is practically one enormous mouth."

3. *Effect of the Removal of Checks.*—The enormous destruction caused by these checks on population may be realized to some extent if we consider the birth rate.

It may be stated as a general rule that the birth rate in existing species is proportional to the rate of destruction. Thus the petrel, which nests on inaccessible cliffs and has few enemies, produces but one egg at a time. While the lobster, whose young are exposed to the attacks of innumerable enemies from the time they are hatched, produces from 3,000 to 90,000 eggs. (The largest number found by Herrick was 97,440, "The Lobster," p. 51.) A single carrion fly is said to produce 20,000 living maggots. These reach full size in five days, and the pupa stage lasts five days. It has been estimated that a single fly could produce in three months one hundred millions of millions of millions (Wallace, "Darwinism," p. 25). The common mosquito (*Culex pungens*) lays from 200 to 400 eggs in a bunch. These hatch in sixteen hours. Under favorable conditions the larvæ reach the pupa stage in seven or eight days. This stage lasts two days. Thus one pair of mosquitoes may produce 400 adult offspring in less than ten days. In a few days more these are ready to lay eggs in their turn.

According to Merriam, the house sparrow produces annually five or six broods of four to six each. Assuming an average of 24 young per annum, with sexes

equally divided, the produce of a single pair in ten years will be 275,716,983,698 ("Agricultural Report," 1886).

The elephant is said to be the slowest breeder of all animals. Yet Darwin has estimated that if an elephant lives 100 years and produces 6 young ones, in 750 years the produce of one pair would equal 19,000,000 elephants. Man is also an extremely slow-breeding animal, yet the human population tends to double in about twenty-five years.

The power of rapid multiplication is perhaps best illustrated by the waves of life that sometimes sweep over a country. Brehm thus describes one of these waves (Brehm, "From North Pole to Equator," 1896, pp. 74-76).

In a description of the fauna of the tundra, or barren lands of northern Siberia, Brehm says: "He (the lemming), or at least his tracks, may be seen everywhere throughout the tundra. The tracks run in all directions, often through places overgrown by dwarf birches, narrow, smooth, neatly kept paths in the moss, going straight for several yards, then diverging to right or left, and only returning to the main path after many circuits. On these we may often see, in great numbers during a dry summer, a little short-tailed, hamster-like animal nimbly pattering along and soon disappearing out of sight. This is the lemming, a rodent smaller than a rat, but larger than a mouse, with a brightly but irregularly marked skin, usually brown, yellow, gray, and black. If we dissect the animal we see, not without surprise, that it consists almost entirely of skin and viscera. Its bones and muscles are fine and tender; its viscera, especially the alimentary and reproductive organs, are enormously developed. This state of things explains some phenomena of its life which were long considered unintelligible; the almost abrupt occurrence of wellnigh unlimited fertility, and the vast, apparently organized migrations of the animal. In ordinary circumstances the lemming leads a very comfortable life. Neither in summer nor in winter has he any anxiety about subsistence. In winter he devours all sorts of vegetable matter—moss-tips, lichen, and bark—in summer he lives in his burrow, in winter in a warm, thick-walled, softly-lined nest. Danger, indeed, threatens from all sides, for not only beasts and birds of prey, but even the reindeer devour hundreds and thousands of lemmings; nevertheless, they increase steadily and rapidly, until special circumstances arise when millions, which have come into existence within a few weeks, are annihilated within a few days. Spring sets in early, and a more than usually dry summer prevails in the tundra. All the young of the first litter of the various lemming females thrive, and in six weeks, at the most, these also multiply. Meantime the parents have brought forth a second and a third litter, and these in turn bring forth young. Within three months the heights and low grounds of the tundra teem with lemmings, just as our fields do with mice under similar circumstances. Whichever way we turn, we see the busy little creatures, dozens at a glance, thousands in the course of an hour. They run about on all the paths and roads; driven to extremity, they turn snarling and sharpening their teeth, on the defensive even against man, as if their countless numbers lent to each individual a defiant courage. But the countless and still increasing numbers prove their own destruction. Soon the lean tundra ceases to afford employment enough for their greedy teeth. Famine threatens, perhaps actually sets in. The anxious animals crowd together and begin their march. Hundreds join with hundreds, thousands with other thousands; the troops become swarms, the swarms armies. They travel in a definite direction, at first following old tracks, but soon striking out on new ones; in unending file, defying all computation, they hasten onward; over the cliffs they plunge into the water. Thousands fall victims to want and hunger; the army behind streams on over their corpses; hundreds of thousands are drowned in the water or are shattered at the foot of the cliffs; the remainder speed on; other hundreds and thousands fall victims to the voracity of Arctic and red foxes,

wolves, and gluttons, rough-legged buzzards and ravens, owls and skuas, which have followed them; the survivors pay no heed. Where they go, how they end, none can say, but certain it is that the tundra behind them is as if dead, that a number of years pass ere the few who have remained behind, and have managed to survive, slowly multiply, and visibly re-people their native fields."

Hudson describes a similarly rapid increase of mice on the Pampas of South America, which was finally brought to a close by a drought and the increase of enemies ("Naturalist in La Plata," p. 59, *et seq.*).

This country is subject to periodic waves of locusts and chinch bugs, which swarm at such times in hundreds of thousands and do enormous damage to crops (Webster, "The Chinch-Bug," 1898). With the introduction of irrigation and forage plants in the far West, the jack-rabbits have increased rapidly and become a pest. In California during the ten years from 1888 to 1897, 494,634 jack-rabbits were killed in "drives," and yet the total number living was not seriously diminished (Palmer, "Jack-Rabbits," 1897).

The power of rapid multiplication is also well illustrated by the effect of introducing animals and plants into a new country. If the climate be favorable, the introduced form, freed from its natural enemies, may often increase amazingly.

Many of our common weeds, like the ox-eye daisy and the so-called Russian thistle, are good examples of this. Wallace gives a number of cases ("Darwinism," p. 28) of the rapid spread of European plants introduced into South America, New Zealand, and other places.

"Columbus in his second voyage left a few black cattle at San Domingo, and these ran wild and increased so much that twenty-seven years afterward herds of from four thousand to eight thousand head were not uncommon. Cattle were afterward taken from this island to Mexico and other parts of America, and in 1587, sixty-five years after the conquest of Mexico, the Spaniards exported 64,350 hides from that country and 35,444 from San Domingo. . . . In the pampas of Buenos Ayres there were at the end of the last century, about twelve million cows and three million horses, besides great numbers in other parts of America." Similar results were obtained by setting free hogs and asses. Camels even, turned loose in Texas not many years ago, increased so rapidly as to become a nuisance.

The common European rabbit has become a pest in Australia and New Zealand. The rabbits were first liberated near Melbourne about 1864, and later in Tasmania and New Zealand. They multiplied so rapidly that in 1879 the legislature of South Australia took action for their destruction, and the matter was taken up soon after in New South Wales, Queensland, New Zealand, and Tasmania. But in spite of all efforts to destroy them, they continued to multiply. Between 1873 and 1898 New Zealand exported two hundred million rabbit skins.

Another example of the rapid increase of an introduced animal is afforded by the Indian mongoose in the West Indies. But at our very doors we have an equally good example in the house sparrow. The first successful importation was made into Brooklyn in 1852. The birds were introduced into Portland, Me., in 1854, and into Providence, R. I., in 1858, some escaping in Boston. Between 1863 and 1870 they were imported into eight cities, one lot of one thousand being sent to Philadelphia. Between 1870 and 1880 it is estimated that the range of this species had been extended by 16,000 square miles (Palmer, 1898), and it has continued to spread. Merriam estimates the rate of spreading of the sparrow as follows ("Agri. Rept.," 1886, p. 238):

	Square miles.
1870-75	500
1875-80	15,640
1880-85	500,760
During 1886	516,500
Yearly average United States and Canada	69,000

4. *Competition.*—These examples will suffice to show how rapidly animals and plants can multiply when the

first two classes of checks on population are not in operation. But this rate of multiplication cannot continue indefinitely. For, finally, food supply will become exhausted or the individuals will become so crowded as to deprive one another of the light, air, or space necessary for life. Thus the tendency of organisms to increase in geometrical ratio, if not held in check by other causes, will ultimately cause a severe competition, and this constitutes the third class of checks on population.

Competition may be between individuals of the same species, or between different species having similar habits. It is well illustrated in the forests, where each tree that reaches its full growth is, according to Pinchot, "the survivor of hundreds (or sometimes even of thousands) of seedlings."

An example where the competition of species has had a marked effect on the flora is quoted by Wallace (pp. 20-22). M. Hansten-Blangsted gives an account of the struggle between the trees in the forests of Denmark. The chief combatants are the beech and the birch, the beech being everywhere successful in its invasions. "Forests composed wholly of birch are now found only in sterile sandy tracts; everywhere else the trees are mixed, and wherever the soil is favorable, the beech rapidly drives out the birch. The latter loses its branches at the touch of the beech, and devotes all its strength to the upper part, where it towers above the beech. It may live long in this way, but it succumbs ultimately in the fight of old age, if of nothing else, for the life of the birch in Denmark is shorter than that of the beech." The superiority of the beech appears to be due to its denser shade. Nothing can live beneath it, while it grows perfectly well under the shade of the birch. The birch has been saved from total extinction only by the fact that it had possession of the Danish forests long before the beech ever reached the country, and that certain districts are unfavorable to the growth of the latter.

But we need not go to Denmark to witness a struggle of this kind. In Virginia, when a field is abandoned, trees soon spring up of all kinds, but the pines by virtue of their more rapid growth and dense shade, soon acquire the ascendancy. Many "old fields" are to be seen where the furrows of the last crop of corn are still visible, and the ground is covered with a thick growth of young pines. Many of these die while still small, and among them may be found a few slender oaks, chestnuts, and tulip trees. If the pines are cut, or if they are allowed to grow old and fall down with decay, their place is taken at once by the longer-lived and more hardy oaks and chestnuts. So that it is a common saying in Virginia that "oaks follow pines."

Another case in point is an experiment of Darwin's. He marked out a little plot of mown turf, three by four feet, and allowed the plants to grow up freely. The result was that out of twenty species growing there nine perished ("Origin of Species," vol. i., p. 83).

Among animals the birds show especially the effect of competition. In some species each pair requires a certain area for a feeding ground, and drives off all others. The English sparrow is said to be responsible to a considerable extent for the decrease of our native birds, and according to a recent writer in *Nature* (Allchin, January 19th, 1899, p. 271), this same sparrow has had a similar effect upon the swallows and martins in England.

The efficiency of competition in checking increase is shown when the competition is lessened by an enlargement of the food supply. Most of the waves of life that have just been described are due to such an advantage rather than to protection from enemies.

In order to understand the results of these factors in the struggle for existence, it must be remembered that, as a rule, the relations of organisms to one another are highly complex; so that any change in the environment of one species is apt to effect a host of others. Thus, according to Lintner, the English sparrow protects the tussock moth (*Orgyia leucostigma*) by driving away its enemies, the robbin, oriole, and cuckoo, the only birds that can feed upon the hairy caterpillars, and thus the spar-

row indirectly injures the elms and other trees ("Agric. Rept.," 1886). The classical example of this is Darwin's one of the relations of cats to the crop of clover seed. He says: "I have also found that the visits of bees are necessary for the fertilization of some kinds of clover; for instance, twenty heads of Dutch clover (*Trifolium repens*) yielded 2,290 seeds, but twenty other heads protected from bees produced not one. Humble bees alone visit red clover, as other bees cannot reach the nectar. Hence we may infer as highly probable 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 Colonel 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 Colonel 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."

Wallace quotes an example from Sir Charles Lyell. He says: "If, by the attacks of seals or other marine foes, salmon are reduced in number, the consequence will be that otters living far inland will be deprived of food and will then destroy many young birds or quadrupeds, so that the increase of a marine animal may cause the destruction of many land animals hundreds of miles away." Another example of complexity of relations between organisms is given by Darwin: "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 of the land having been enclosed, so that cattle could not enter."

These examples are enough to show how very complex are the relations of organisms to one another. We see how a change in the environment of the salmon produces a change in the environment of land animals far away, and how the introduction of a single tree and the exclusion of cattle profoundly affect a host of other organisms. This gives some idea of the complexity of the phenomena to be considered in a discussion of the origin of species.

**Natural Selection.**—The facts of variation, inheritance, and the struggle for existence lead, as Darwin and Wallace pointed out, to the *a priori* assumption of the theory of natural selection. If individuals differ in their characteristics, and if there is a struggle for existence in which many perish, then there may be a correlation between the death rate and certain structural or physiological peculiarities, that is, we shall have a survival of the fittest, or better, an elimination of the least fit. But in order that new species may result, not only must the favorable peculiarities of the survivors be transmitted to future generations by inheritance, but other conditions must be fulfilled which we will now consider.

In the first place, as indicated in the preceding para-

graph, it by no means follows that there is any necessary relation between destruction and any structural or physiological peculiarity. A flood, a tornado, a forest fire may destroy all in its path. In such a case the destruc-

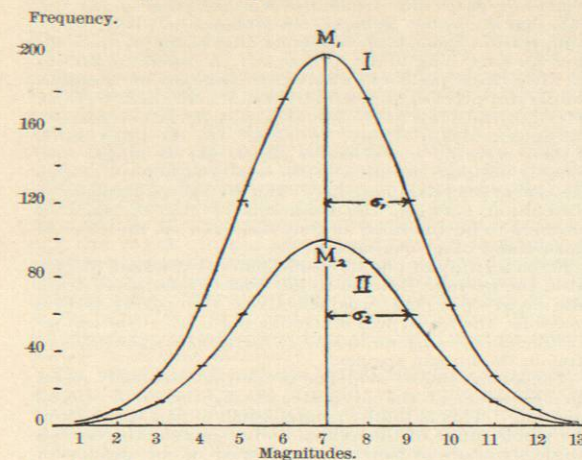


FIG. 1947.—Fortuitous Destruction of 500 in 1,000, Normal Curves. I, Birth curve; II, survival curve.

tion is purely fortuitous, or non-selective. On the other hand, if a number of persons are exposed to an infection, say typhoid, to which they present different degrees of susceptibility, then those which possess those physiological characteristics that give susceptibility to the disease in the greatest degree will be those that die, and we shall have then a *selective death rate*. It may be noted in passing that a death rate which is selective in regard to one character may be fortuitous in respect to another, unless the variations of the two characters are correlated.

Let us consider now what the effect of these two kinds of destruction would be upon the curve of variation. Where there is no destruction, and all that are born sur-

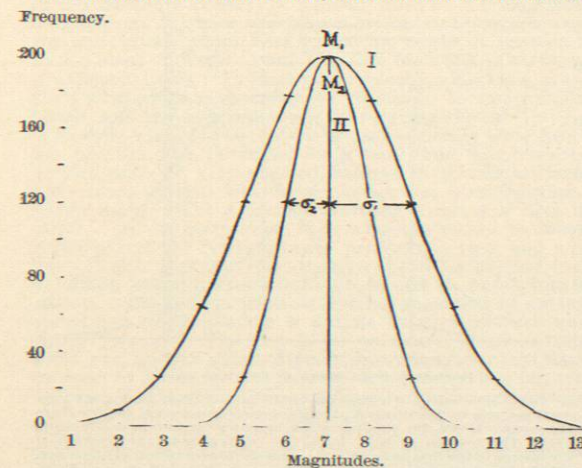


FIG. 1948.—Selective Death Rate of 500 in 1,000 when the Birth and Survival Means Coincide, Normal Curves. I, Birth curve; II, survival curve.

vive, we may call the curve the *birth curve*, and its mean the *birth mean*. While the curve obtained after destruction had taken place would be the *survival curve*, and its mean, the *survival mean*. Now the effect of purely for-

titous destruction would be to give a survival curve that would be exactly like the birth curve except that it would be flatter, and the birth mean and the survival mean would coincide. Such a case is illustrated by Fig. 1947, where the upper line (I) may be taken to represent the birth curve of say a thousand individuals in a certain locality, and the lower line (II) would be the curve after a fortuitous destruction of half the number. (If percentages were used instead of absolute numbers, the curves would be exactly alike.)

The effect of a selective death rate upon the birth curve would depend upon whether the cause of death is a constant factor of the environment or a new one. If it be a constant factor, it is probable that the species has become adjusted to it. In this case the most favorable variation of any character affected by this condition will be represented by the mode, and probably the mean, of the birth curve. Elimination will cause a decrease of variability, so that the survival curve will be steeper on the sides than the birth curve (Fig. 1948). But the position of the mean will not be changed, and there will be no evolution. On the contrary, the effect of natural selection here will be, if anything, to make the species more stable.

It is only when the species as a whole is not adjusted

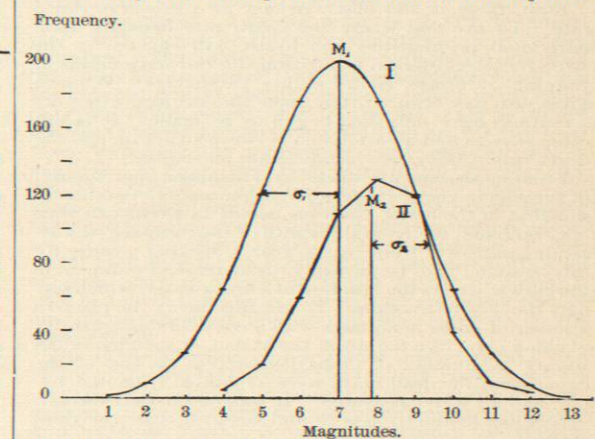


FIG. 1949.—Selective Death Rate of 500 in 1,000 where the Birth and Survival Mean do not Coincide. I, Birth curve, normal; II, survival curve, purely imaginary.

to the cause of death that we may expect natural selection to produce evolution. Then the birth mean will not coincide with the most favorable variation, and the effect of elimination will be to decrease the variability to a greater extent upon the less favorable side than on the other and thus to shift the mean, as in Fig. 1949. This is a purely imaginary example, where the most favorable value of the character measured is supposed to be 9. It will be noticed that the effect of elimination here has been to shift the mean from 7 to 7.88, that is toward 9, and the variability is decreased as shown by the smaller value of the standard deviation,  $\sigma_2$ , which is 1.46 instead of 2. The survival curve is also skew, while the birth curve is supposed to have been symmetrical.

So far we have dealt with the effect of selection upon the first generation only. Of course, fortuitous destruction will have no effect upon the type or variability of the next generation, for the type and variability of the parents have remained unchanged. A selective death rate symmetrical on both sides of the birth mean will not affect the type and will have but a slight effect upon the variability, for Pearson has shown that selection for an indefinite number of generations cannot reduce the variability more than eleven per cent. But where the most favorable value of a character does not coincide with the birth mean, then there will be a change of type, the rapidity of change depending upon the severity of the se-