1. *On the Tendency of Species to Form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection.*

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Communicated by Sir Charles Lyell, F.R.S., F.L.S., and J. D. Hooker, Esq., M.D., V.P.R.S., F.L.S., &c.

[READ JULY 1ST, 1858]

London, June 30th, 1858.

My Dear Sir—The accompanying papers, which we have the honor of communicating to the Linnean Society, and which all relate to the same subject, viz. the Laws which affect the Production of Varieties, Races and Species, contain the results of the investigations of two indefatigable naturalists, Sir Charles Darwin and Mr. Alfred Wallace.

These gentlemen having, independently and unknown to one another, conceived the same very ingenious theory to account for the appearance and perpetuation of varieties and of specific forms on our planet, may both fairly claim the merit of being original thinkers in this important line of inquiry; but neither of them having published his views, though Mr. Darwin has for many years past been repeatedly urged by us to do so, and both authors having now unreservedly placed their papers in our hands, we think it would best promote the interests of science that a selection from them should be laid before the Linnean Society.[1]

Taken in the order of their dates, they consist of:—

1. Extracts from a MS. work on Species,[a] by Mr. Darwin, which was sketched in 1839, and copied in 1844, when the copy was read by Dr. Hooker, and its contents afterwards communicated to Sir Charles Lyell. The first Part is devoted to "The Variation of Organic Beings under Domestication and in their Natural State"; and the second chapter of that Part, from which we propose to read to the Society the extracts referred to, is headed, "On the Variation of Organic Beings in a state of Nature; on the Natural Means of Selection; on the Comparison of Domestic Races and true Species."

2. An abstract of a private letter addressed to Professor Asa Gray, of Boston, U.S., in October 1857, by Mr. Darwin, in which he repeats his views, and which shows that these remained unaltered from 1839 to 1857.

3. An Essay by Mr. Wallace, entitled "On the Tendency of Varieties to depart indefinitely from the Original Type." This was written at Ternate[2] in February 1858, for the perusal of his friend and correspondent Mr. Darwin, and sent to him with the expressed wish that it should be forwarded to Sir Charles Lyell, if Mr. Darwin thought it sufficiently novel and interesting. So highly did Mr. Darwin appreciate the value of the views therein set forth, that he proposed, in a letter to Sir Charles Lyell, to obtain Mr. Wallace's

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[1] Charles Darwin began to formulate his thoughts on natural selection soon after he returned from his voyage on the *Beagle* in 1836. However, he kept his ideas on what he called the "species problem," secret from all but a few trusted associates. Because Darwin's letters from the field had been read before the Cambridge Philosophical Society and the Geological Society of London, he was already a celebrity in scientific circles by the time he returned home. During the late 1830s and early 1840s, Darwin achieved a measure of fame from a series of popular books he authored about South American geology and zoology. Yet at the same time he was secretly compiling data for his theory of evolution through discussions with gardeners, animal breeders, and naturalists. In his autobiography, Darwin wrote that these ideas crystallized into his theory of natural selection after he read Thomas Malthus' "Essay on the Principle of Population as It Affects the Future Improvement of Society" in 1838.

[2] Ternate is a city in the northern Moluccas, now part of Indonesia.

consent to allow the essay to be published as soon as possible. Of this step we highly approved, provided Mr. Darwin did not withhold from the public, as he was strongly inclined to do (in favour of Mr. Wallace), the memoir which he had himself written on the same subject, and which, as before stated, one of us had perused in 1844, and the contents of which we had both of us been privy to for many years.[3] On representing this to Mr. Darwin, he gave us permission to make what use we thought proper of his memoir, &c.; and in adopting our present course, of presenting it to the Linnean Society, we have explained to him that we are not solely considering the relative claims to priority of himself and his friend, but the interests of science generally; for we feel it to be desirable that views founded on a wide deduction from facts, and matured by years of reflection, should constitute at once a goal from which others may start, and that, while the scientific world is waiting for the appearance of Mr. Darwin's complete work, some of the leading results of his labours, as well as those of his able correspondent, should together be laid before the public.

We have the honor to be yours very obediently,
Charles Lyell
Jos. D. Hooker

J. J. Bennett, Esq.,
Secretary of the Linnean Society.

I. Extract from an unpublished work on Species, by C. Darwin Esq., consisting of a portion of a Chapter entitled "On the variation of Organic Beings in a state of Nature; on the Natural Means of Selection; on the Comparison of Domestic Races and true Species."

De Candolle, in an eloquent passage, has declared that all nature is at war, one organism with another, or with external nature.[4] Seeing the contented face of nature, this may at first well be doubted; but reflection will inevitably prove it to be true. The war, however, is not constant, but recurrent in a slight degree at short periods, and more severely at occasional more distant periods; and hence its effects are easily overlooked. It is the doctrine of Malthus applied in most cases with tenfold force.[5] As in every climate there are seasons, for each of its inhabitants, of greater and less abundance, so all annually breed; and the moral restraint which in some small degree checks the increase of mankind is entirely lost. Even slow breeding mankind has doubled in twenty-five years; and if he could increase his food with greater ease, he would double in less time. But for animals without artificial means, the amount of food for each species must, *on an average,* be constant, whereas the increase of all organisms tends to be geometrical, and in a vast majority of cases at an enormous ratio. Suppose in a certain spot there are eight pairs of birds, and that only four pairs of them annually (including double hatches) rear *only* four young, and that these go on rearing their young at the same rate, then at the end of seven years (a short life, excluding violent deaths, for any bird) there will be 2048 birds, instead of the original sixteen. As this increase is quite impossible, we must conclude either that birds do not rear nearly half their young, or that the average life of a bird is, from accident, not nearly seven years. Both checks probably concur. The same kind of calculation applied to all plants and animals affords results

[3] As pointed out above, Darwin must have been bitterly disappointed when he received Wallace's letter. However, it was very much within his character to urge publication of his rival's work. Darwin was of a shy and reticent temperament and was frequently sick. Although he elaborated and defended his ideas in print, he left the public defense of his ideas as well as confrontational debate to others, particularly his friends Joseph Dalton Hooker and Thomas Henry Huxley (1825–1895). Huxley was so aggressive in his defense of Darwin's ideas that he was known as Darwin's Bulldog.

[4] De Candolle (1806–1893) was a Swiss botanist who discussed the concept of life as a struggle for existence well before Darwin outlined his theory of natural selection, and Darwin credits De Candolle's work as a direct influence on his work. Although Darwin did not read French well, he was an avid student of the geologist Charles Lyell, and Lyell quoted De Candolle extensively in the third volume of his 1834 book *Principles of Geology* (Eisley 1961:101).

[5] Thomas Robert Malthus (1766–1834) was a critical influ-

more or less striking, but in very few instances more striking than in man.

Many practical illustrations of this rapid tendency to increase are on record, among which, during peculiar seasons, are the extraordinary numbers of certain animals; for instance, during the years 1826 to 1828, in La Plata, when from drought some millions of cattle perished, the whole country actually *swarmed* with mice.[6] Now I think it cannot be doubted that during the breeding-season all the mice (with the exception of a few males or females in excess) ordinarily pair, and therefore that this astounding increase during three years must be attributed to a greater number than usual surviving the first year, and then breeding, and so on till the third year, when their numbers were brought down to their usual limits on the return of wet weather. Where man has introduced plants and animals into a new and favourable country, there are many accounts in how surprisingly few years the whole country has become stocked with them. This increase would necessarily stop as soon as the country was fully stocked; and yet we have every reason to believe, from what is known of wild animals, that *all* would pair in the spring. In the majority of cases it is most difficult to imagine where the checks fall—though generally, no doubt, on the seeds, eggs, and young; but when we remember how impossible, even in mankind (so much better known than any other animal), it is to infer from repeated casual observations what the average duration of life is, or to discover the different percentage of deaths to births in different countries, we ought to feel no surprise at our being unable to discover where the check falls in any animal or plant. It should always be remembered, that in most cases the checks are recurrent yearly in a small, regular degree, and in an extreme degree during unusually cold, hot, dry, or wet years, according to the constitution of the being in question. Lighten any check in the least degree, and the geometrical powers of increase in every organism will almost instantly increase the average number of the favoured species. Nature may be compared to a surface on which rest ten thousand sharp wedges touching each other and driven inwards by incessant blows. Fully to realize these views much reflection is requisite. Malthus on man should be studied; and all such cases as those of the mice in La Plata, of the cattle and horses when first turned out in South America, of the birds by our calculation, &c., should be well considered. Reflect on the enormous multiplying power *inherent and annually in action* in all animals; reflect on the countless seeds scattered by a hundred ingenious contrivances, year after year, over the whole face of the land; and yet we have every reason to suppose that the average percentage of each of the inhabitants of a country usually remains constant. Finally, let it be borne in mind that this average number of individuals (the external conditions remaining the same) in each country is kept up by recurrent struggles against other species or against external nature (as on the borders of the arctic regions, where the cold checks life), and that ordinarily each individual of every species holds its place, either by its own struggle and capacity of acquiring nourishment in some period of its life, from the egg upwards; or by the struggle of its parents (in short-lived organisms, when the main check occurs at longer intervals)

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ence on Darwin. In 1798, Malthus had published "An Essay on the Principles of Population as It Affects the Future Improvement of Society with Remarks on the Speculations of Mr. Godwin, M. Condorcet and Other Writers." In this work Malthus observes that without interference, a species' population will grow geometrically (a sequence such as 1, 2, 4, 8, 16, 32), but the food supply will only grow arithmetically (a sequence such as 1, 3, 5, 7, 9, 11). According to Malthus, this showed that individuals and groups had inevitably to struggle over a limited food supply. Darwin adopts Malthus' essential insight: that creatures struggle and compete to survive. In this and succeeding paragraphs, Darwin elaborates and extends this idea. He points to environmental factors such as food supply, climate, and competition between organisms for limited resources that act as checks on population growth, and thus as the agents of natural selection.

[6] La Plata (in Argentina) was one of the first places Darwin visited on his *Beagle* voyage, arriving there in the summer of 1832, some years after the mouse infestation.

with other individuals of the *same* or *different* species.[7]

But let the external conditions of a country alter. If in a small degree, the relative proportions of the inhabitants will in most cases simply be slightly changed; but let the number of inhabitants be small, as on an island, and free access to it from other countries be circumscribed, and let the change of conditions continue progressing (forming new stations), in such a case the original inhabitants must cease to be as perfectly adapted to the changed conditions as they were originally.[8] It has been shown in a former part of this work, that such changes of external conditions would, from their acting on the reproductive system, probably cause the organization of those beings which were most affected to become, as under domestication, plastic.[9] Now, can it be doubted, from the struggle each individual has to obtain subsistence, that any minute variation in structure, habits, or instincts, adapting that individual better to the new conditions, would tell upon its vigour and health? In the struggle it would have a better *chance* of surviving; and those of its offspring which inherited the variation, be it ever so slight, would also have a better *chance*. Yearly more are bred than can survive; the smallest grain in the balance, in the long run, must tell on which death shall fall and which shall survive. Let this work of selection on the one hand, and death on the other, go on for a thousand generations, who will pretend to affirm that it would produce no effect, when we remember what, in a few years, Bakewell effected in cattle, and Western in sheep, by this identical principle of selection?[10]

To give an imaginary example from changes in progress on an island:—let the organization of a canine animal which preyed chiefly on rabbits, but sometimes on hares, become slightly plastic; let these same changes cause the number of rab-

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[7] Darwin conceived of natural selection as a contest or battle for survival. For example, he often talks about an organism's "struggle" for survival. In particular, he believed that struggle might be most severe between members of the same species, because they are in direct competition. Whereas, members of different species are often dependent on each other.

[8] Here Darwin is clearly thinking of his experiences in the Galapagos. That Darwin came to much of his understanding of evolution as a result of his visit to the Galapagos is well known. Less well known is the fact that he came to understand the importance of the Galapagos only after he had left the islands. For example, according to his *Journal of Researches* (1839), Darwin was very surprised when Lawson, the vice-governor of the Galapagos Islands, called his attention to the interisland variation among finches. To his chagrin, Darwin discovered he had not sorted many of his finch specimens by the island on which they were found.

[9] This essay is derived from the work that would be published as *On the Origin of Species*. When Darwin writes, "In a former part of this work . . . ," he is referring to the discussion of his research into domestication of plants and animals that appears in the first chapter of *Origin of Species*. In *On the Origin of Species,* he writes, "Breeders habitually speak of an animal's organization as something quite plastic, which they can model almost as they please" (1964:31). One weakness of Darwin's work is that he was unable to understand the mechanisms of inheritance and the limits of variation. This is not surprising since he wrote before Gregor Mendel (1822–1884) reported his findings on heredity. Mendel's work was published in 1866, but went unnoticed by biologists until 1900.

[10] Here, near the beginning of the essay, Darwin outlines the basic elements in his theory of natural selection:

a. There is physical variation within species.
b. Populations grow geometrically but only a few offspring survive to adulthood.
c. Organisms compete for survival.

Natural selection states that some individuals in a population possess variations (adaptations) that give them an advantage over others in their competition for survival and procreation. This allows them to survive while others perish. The environment will "naturally select" those individuals with adaptive variations over those without the advantageous traits.

The mention of Bakewell and Western in the last sentence of this paragraph is a reference to Robert Bakewell (1725–1795) and Lord Charles Callis Western (1767–1844). These were among the first Englishmen to practice the selective breeding of livestock to exaggerate commercially desirable traits.

bits very slowly to decrease, and the number of hares to increase: the effect of this would be that the fox or dog would be driven to try to catch more hares: his organization, however, being slightly plastic, those individuals with the lightest forms, longest limbs, and best eyesight, let the difference be ever so small, would be slightly favoured, and would tend to live longer, and to survive during that time of the year when food was scarcest; they would also rear more young, which would tend to inherit these slight peculiarities. The less fleet ones would be rigidly destroyed. I can see no more reason to doubt that these causes in a thousand generations would produce a marked effect, and adapt the form of the fox or dog to the catching of hares instead of rabbits, than that greyhounds can be improved by selection and careful breeding. So would it be with plants under similar circumstances. If the number of individuals of a species with plumed seeds could be increased by greater powers of dissemination within its own area (that is if the check to increase fell chiefly on the seeds), those seeds which were provided with ever so little more down, would in the long run be most disseminated; hence a greater number of seeds thus formed would germinate, and would tend to produce plants inheriting the slightly better-adapted down.[b]

Besides this natural means of selection, by which those individuals are preserved, whether in their egg, or larval, or mature state, which are best adapted to the place they fill in nature, there is a second agency at work in most unisexual animals, tending to produce the same effect, namely, the struggle of the males for the females. These struggles are generally decided by the law of battle, but in the case of birds, apparently, by the charms of their song, by their beauty or their power of courtship, as in the dancing rock-thrush of Guiana. The most vigorous and healthy males, implying perfect adaptation, must generally gain the victory in their contests. This kind of selection, however, is less rigorous than the other; it does not require the death of the less successful, but gives to them fewer descendants. The struggle falls, moreover, at a time of year when food is generally abundant, and perhaps the effect chiefly produced would be the modification of the secondary sexual characteristics, which are not related to the power of obtaining food, or to defense from enemies, but to fighting with or rivaling other males. The result of this struggle amongst the males may be compared in some respects to that produced by those agriculturists who pay less attention to the careful selection of all their young animals, and more to the occasional use of a choice mate.[11]

II. Abstract of a Letter from C. Darwin, Esq., to Prof. Asa Gray, Boston, U.S., dated Down, September 5th, 1857.[12]

1. It is wonderful what the principle of selection by man, that is the picking out of individuals with any desired quality, and breeding from them, and again picking out, can do. Even breeders have been astounded at their own results. They can act on differences inappreciable to the unaided eye. Selection has been *methodically* followed in *Europe* for only the last half century; but it was occasionally, and even in some degree methodically followed in the most ancient times. There must have been also a kind of unconscious

[11] In this critical paragraph, Darwin points out that there are two different selection processes going on in nature. In the first, natural selection, individuals compete for access to food and environmental locations. In the second, sexual selection, they compete for access to mates.

Although Darwin uses the word "struggle" in this paragraph and speaks of the "law of battle," conjuring up images of great beasts fighting for survival, that is not necessarily the picture Darwin wanted to paint. Essentially, he tells us that evolutionary success is indicated by the number of offspring an organism produces. Thus, "success" goes to the most prolific breeders, not necessarily to the biggest, strongest, and fastest individuals. This is contrary to the popular image of evolution. In the case of birds, the "charm of their song," for example, may convey a selective advantage.

[12] Asa Gray (1810–1888) was an eminent American botanist and the author of *Gray's Manual of Botany,* a standard textbook in that field. As chair of natural history at Harvard, he was a strong supporter of Darwin's ideas.

selection from a remote period, namely in the preservation of the individual animals (without any thought of their offspring) most useful to each race of man in his particular circumstances. The "roguing," as nurserymen call the destroying of varieties which depart from their type, is a kind of selection. I am convinced that intentional and occasional selection has been the main agent in the production of our domestic races; but however this may be, its great power of modification has been indisputably shown in later times. Selection acts only by the accumulation of slight or greater variations, caused by external conditions, or by the mere fact that in [every] generation the child is not absolutely similar to its parent. Man, by this power of accumulating variations, adapts living beings to his wants — may be said to make the wool of one sheep good for carpets, of another for cloth, &c.[13]

2. Now suppose there were a being who did not judge by mere external appearances, but who could study the whole internal organization, who was never capricious, and should go on selecting for one object during millions of generations; who will say what he might not effect?[14] In nature we have some slight variation occasionally in all parts; and I think it can be shown that changed conditions of existence is the main cause of the child not exactly resembling its parents; and in nature geology shows us what changes have taken place, and are taking place. We have almost unlimited time; no one but a practical geologist can fully appreciate this. Think of the Glacial period, during the whole of which the same species at least of shells have existed; there must have been during this period millions on millions of generations.[15]

3. I think it can be shown that there is such all unerring power at work in *Natural Selection* (the title of my book), which selects exclusively for the good of each organic being. The elder De Candolle, W. Herbert, and Lyell have written

[13] Much of the data Darwin cited in support of his theory was collected by observing commercial plant and animal breeders. Here he notes one of the most important foundations of his theory: the notion that in every species, in every generation there is great variation. As he points out, "the child is not absolutely similar to its parent."

[14] Darwin believed that natural selection was both physically and morally progressive and in the first sentence of this paragraph, one can glimpse a hint of that assumption. Although humans are virtually unmentioned in *Origin of Species,* Darwin believed natural selection acted on us as well. Could his mention of a being who did not judge by external appearance, was never capricious, and could select for traits over millions of generations be a reference to his belief that God arrived at humans through natural selection? Darwin, after all, had originally gone to Cambridge University to study for the ministry.

Although Darwin's conviction that evolution is progressive has made its way into popular belief in the assumption that modern organisms (especially humans) are more advanced, complex, and diverse than in the past, this view is not a necessary part of modern evolutionary theory. Complex life-forms of one sort or another have existed for hundreds of millions of years, and, according to Harvard biologist Stephen J. Gould (1989), the greatest diversity of life-forms was found 570 million years ago, during the Cambrian period. Evolutionary history, since then, has been marked by mass extinctions of life-forms.

The belief in the progressive nature of evolution was widely accepted during the latter half of the nineteenth and the first half of the twentieth centuries. The application of progressivist evolutionary frameworks to human societies, called social darwinism, had widespread social consequences. Following Spencer's idea of the "survival of the fittest," social darwinists argued that the technological advantages of Western European and American society were clear evidence of their evolutionary superiority. This belief was generalized to support the racist assumption that Northern Europeans were morally and intellectually superior to others. Within Western society, this belief was used to argue that wealthy upper-class individuals were superior to members of the lower class. Spencer even argued against government aid to the poor such as public schools and medical programs in the belief that these policies slowed the progress of human evolution by allowing individuals who were not fit to survive.

Modern biologists view evolution as a random process without purpose or direction. An organism's adaptive trait in one generation may lead to the population's extinction in future generations. In fact, the more evolutionarily specialized a population, the less adaptable it is to changing circumstances and the more vulnerable it may be to extinction.

[15] The geologist Charles Lyell had a profound influence on the work of both Darwin and Wallace. Lyell is best known for his book *Principles of Geology* (1834), in which he

excellently on the struggle for life; but even they have not written strongly enough. Reflect that every being (even the elephant) breeds at such a rate, that in a few years, or at most a few centuries, the surface of the earth could not hold the progeny of one pair. I have found it hard constantly to bear in mind that the increase of every single species is checked during some part of its life, or during some shortly recurrent generation. Only a few of those annually born can live to propagate their kind. What a trifling difference must often determine which shall survive, and which perish![16]

4. Now take the case of a country undergoing some change. This will tend to cause some of its inhabitants to vary slightly—not but that I believe most beings vary at all times enough for selection to act on them. Some of its inhabitants will be exterminated; and the remainder will be exposed to the mutual action of a different set of inhabitants, which I believe to be far more important to the life of each being than mere climate. Considering the infinitely various methods which living beings follow to obtain food by struggling with other organisms, to escape danger at various times of life, to have their eggs or seeds disseminated, &c. &c., I cannot doubt that during millions of generations individuals of a species will be occasionally born with some slight variation, profitable to some part of their economy. Such individuals will have a better chance of surviving, and of propagating their new and slightly different structure; and the modification may be slowly increased by the accumulative action of natural selection to any profitable extent. The variety thus formed will either coexist with, or, more commonly, will exterminate its parent form. An organic being, like the woodpecker or misseltoe, may thus come to be adapted to a score of contingencies—natural selection accumulating those slight variations in

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amassed voluminous geological evidence in support of the theory of uniformitarianism first proposed by the eighteenth-century Scottish geologist James Hutton (1726–1797). Hutton argued that the geological processes we observe today, such as erosion and volcanism, were responsible for the geological features of Earth. This was a controversial idea, for it contradicted a popular theory called catastrophism that supported the biblical account of Genesis. Catastrophism was cited to explain how geological features could have been formed in the short period of time since God's creation of Earth, estimated, by Archbishop James Ussher (1581–1656), to have occurred in 4004 B.C.

An important aspect of the doctrine of uniformitarianism that Darwin incorporated into his theory of evolution was the notion of gradualism, the idea that it must have taken the processes of nature a very long time to form Earth's geological features. Gradualism affected Darwin's theory in several ways. First, if the features of Earth were formed gradually rather than by catastrophe, then the process must have taken a very long time, much longer than the 6,000 years proposed by the catastrophists. Darwin had to explain how the diversity of life-forms that existed on Earth had evolved in the time since the creation. Lyell's theory, by showing that Earth was very old, provided the time frame necessary for natural selection to operate. Second, Darwin adopted the notion of gradualism for his own theory, arguing that evolution proceeded by the slow, steady accumulation of variations over a great many generations to produce new species of plants and animals. In the past several decades, this has proven a controversial aspect of Darwin's work. Although some life-forms do seem to evolve slowly as Darwin suggested, the history of others is characterized by long periods of stasis punctuated by relatively brief episodes of change.

At the end of the paragraph, Darwin refers to shells existing for millions of years. Darwin was an avid collector of fossils during his years on the *Beagle*. One critical experience that, for Darwin, confirmed the truth of Lyell's notion of uniformitarianism and gradualism was his discovery of a bed of shells at an elevation higher than 13,000 feet in the Andes.

[16] William Herbert (1778–1847), mentioned here, was an intellectual of his day, largely forgotten now. He was a churchman, poet, folklorist, and an expert on the breeding of plants, particularly amaryllis. He wrote extensively on these subjects. Herbert was the third son of Henry, first earl of Carnarvon. Herbert's son, Henry William Herbert, immigrated to America, where he achieved fame as a sport and nature author under the pseudonym of Frank Forester. Herbert's somewhat distant relation, George Edward Stanhope Molyneux Herbert, the fifth earl of Carnarvon, financed Howard Carter, who discovered the tomb of the Egyptian pharaoh Tutankhamen.

all parts of its structure, which are in any way useful to it during any part of its life.[17]

5. Multiform difficulties will occur to every one, with respect to this theory. Many can, I think, be satisfactorily answered. *Natura non facit saltum*[18] answers some of the most obvious. The slowness of the change, and only a very few individuals undergoing change at any one time, answers others. The extreme imperfection of our geological records answers others.[19]

6. Another principle, which may be called the principle of divergence, plays, I believe, an important part in the origin of species. The same spot will support more life if occupied by very diverse forms. We see this in the many generic forms in a square yard of turf, and in the plants or insects on any little uniform islet, belonging almost invariably to as many genera and families as species. We can understand the meaning of this fact amongst the higher animals, whose habits we understand. We know that it has been experimentally shown that a plot of land will yield a greater weight if sown with several species and genera of grasses, than if sown with only two or three species. Now, every organic being, by propagating so rapidly, may be said to be striving its utmost to increase in numbers. So it will be with the offspring of any species after it has become diversified into varieties, or subspecies, or true species. And it follows, I think, from the foregoing facts, that the varying offspring of each species will try (only few will succeed) to seize on as many and as diverse places in the economy of nature as possible. Each new variety of species, when formed, will generally take the place of, and thus exterminate its less well-fitted parent. This I believe to be the origin of the classification and affinities of organic beings at all times; for organic beings always *seem* to branch and sub-branch like the limbs of a tree from a common trunk, the flourishing and diverging twigs destroying the less vigorous—the dead and lost branches rudely representing extinct genera and families.[20]

This sketch is *most* imperfect; but in so short a space I cannot make it better. Your imagination must fill up very wide blanks.

C. Darwin.

III. On the Tendency of Varieties to Depart Indefinitely from the Original Type. By ALFRED RUSSEL WALLACE.[21]

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

[17] This passage displays additional critical elements of Darwin's theory: the notion that some individuals may be born with adaptive physical characteristics and that they are able to pass these along to their offspring. Thus, in each generation there are fewer individuals who do not have these traits.

The adaptation of organisms to their environment was popularly viewed as evidence of God's workmanship as the master craftsman of life. Here Darwin is using this same line of reasoning to support his belief in the power of natural selection to adapt organisms to their environmental situations.

[18] *Natura non facit saltum:* Nature does not skip steps. Darwin believed that evolution was a slow process involving the accumulation of minute changes. This was a popular notion. E. B. Tylor repeats the same phrase, in French, in essay 3.

[19] Here Darwin indicates that there are difficulties with his theory that he cannot answer. If the history of life is a process of slow change caused by the accumulation of minute variations, then long sequences of fossils should exist to demonstrate these changes. These collections exist today, but in Darwin's day they were incomplete.

[20] Using the image of the branching limbs of a tree, Darwin outlines how his theory of natural selection accounts for evolutionary change over time and illustrates the process of speciation. In *Origin of Species,* Darwin uses branch diagrams to illustrate this process. This has since become a conventional (though perhaps problematic) way to represent evolutionary change.

[21] When Wallace sent his famous letter to Darwin, the two had already been corresponding for two years, and Wallace knew of Darwin's interest in speciation. *Receipt of* Wallace's letter threw Darwin into a quandary. Many of his

the least favourable 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. These conditions will also determine the population of a species; and by a careful consideration of all the circumstances we may be enabled to comprehend, and in some degree to explain, what at first sight appears so inexplicable — the excessive abundance of some species while others closely allied to them are very rare.

The general proportion that must obtain between certain groups of animals is readily seen. Large animals cannot be so abundant as small ones; the carnivora must be less numerous than the herbivora; eagles and lions can never be so plentiful as pigeons and antelopes; the wild asses of the Tartarian deserts cannot equal in numbers the horses of the more luxuriant prairies and pampas of America. The greater or less fecundity of an animal is often considered to be one of the chief causes of its abundance or scarcity; but a consideration of the facts will show us that it really has little or nothing to do with the matter. Even the least prolific of animals would increase rapidly if unchecked, whereas it is evident that the animal population of the globe must be stationary, or perhaps, through the influence of man, decreasing.[22] Fluctuations there may be; but permanent increase, except in restricted localities, is almost impossible. For example, our own observation must convince us that birds do not go on increasing every year in a geometrical ratio, as they would do, were there not some powerful check to their natural increase. Very few birds produce less than two young ones each year, while many have six, eight or ten; four will certainly be below the average; and if we suppose that each pair produce young only four times in their life, that will also be below the average, supposing them not to die either by violence or want of food. Yet at this rate how tremendous would be the increase in a few years from a single pair! A simple calculation will show that in fifteen years each pair of birds would have increased to nearly ten millions! Whereas we have no reason to believe that the number of the birds of any country increases at all in fifteen or in one hundred and fifty years. With such powers of increase the population must have reached its limits, and have become stationary, in a very few years after the origin of each species. It is evident, therefore, that each year an immense number of birds must perish — as many in fact as are born; and as on the lowest calculation the progeny are each year twice as numerous as their parents, it follows that, whatever be the average number of individuals existing in any given country, *twice that number must perish annually,* — a striking result, but one which seems at least highly probable, and is perhaps under rather than over the truth. It would therefore appear that, as far as the continuance of the species and the keeping up the average number of individuals are concerned, large broods are superfluous. On the

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ideas were clearly explained by Wallace. On the one hand, Darwin knew that he could not suppress Wallace's work. On the other, he certainly wanted credit for his own. His response was to consult with his friends, biologist Jonathan Dalton Hooker and geologist Charles Lyell. It is through their efforts that the joint presentation and publication of the Darwin and Wallace essays came about. Wallace, by the way, was not notified of any of this until late 1858, after his work had been published.

Although this first presentation of natural selection credits both Darwin and Wallace, the theory has become much more linked to Darwin's name for several reasons. First, the fact that Darwin had been working for years on the theory was well known in scientific circles in England. Second, Wallace remained in Indonesia until late 1862 and did not publish anything further on evolution until late 1863. By this time Darwin's *On the Origin of Species* had been available for most of four years. Third, while Wallace remained a staunch supporter of most of Darwin's theoretical position, after 1865 he was increasingly committed to spiritualism and argued that while natural selection could account for many aspects of nature, it could not account for the development of human consciousness. This alienated him from many scientists.

[22] Wallace here makes the interesting point that a species' fertility has little to do with its overall population. As we will see below, echoing Malthus, he postulates that food supply is the primary factor regulating population growth, not fecundity. Note that as early as 1858 Wallace recognized that human actions were a factor in the extinction of animal species.

average all above *one* become food for hawks and kites, wild cats and weasels, or perish of cold and hunger as winter comes on. This is strikingly proved by the case of particular species; for we find that their abundance in individuals bears no relation whatever to their fertility in producing offspring. Perhaps the most remarkable instance of an immense bird population is that of the passenger pigeon of the United States which lays only one, or at most two eggs, and is said to rear generally but one young one. Why is this bird so extraordinarily abundant, while others producing two or three times as many young are much less plentiful? The explanation is not difficult. The food most congenial to this species, and on which it thrives best, is abundantly distributed over a very extensive region, offering such differences of soil and climate, that in one part or another of the area the supply never fails. The bird is capable of a very rapid and long-continued flight, so that it can pass without fatigue over the whole of the district it inhabits, and as soon as the supply of food begins to fail in one place is able to discover a fresh feeding ground. This example strikingly shows us that the procuring a constant supply of wholesome food is almost the sole condition requisite for ensuring the rapid increase of a given species, since neither the limited fecundity, nor the unrestrained attacks of birds of prey and of man are here sufficient to check it. In no other birds are these peculiar circumstances so strikingly combined. Either their food is more liable to failure, or they have not sufficient power of wing to search for it over an extensive area, or during some season of the year it becomes very scarce, and less wholesome substitutes have to be found; and thus, though more fertile in offspring, they can never increase beyond the supply of food in the least favourable seasons.[23] Many birds can only exist by migrating, when their food becomes scarce, to regions possessing a milder, or at least a different climate, though, as these migrating birds are seldom excessively abundant, it is evident that the countries they visit are still deficient in a constant and abundant supply of wholesome food. Those whose organization does not permit them to migrate when their food becomes periodically scarce, can never attain a large population. This is probably the reason why woodpeckers are scarce with us, while in the tropics they are among the most abundant of solitary birds. Thus the house sparrow is more abundant than the redbreast, because its food is more constant and plentiful,—seeds of grasses being preserved during the winter, and our farm-yards and stubble-fields furnishing an almost inexhaustible supply. Why, as a general rule, are aquatic, and especially sea birds, very numerous in individuals? Not because they are more prolific than others, generally the contrary; but because their food never fails, the sea-shores and river-banks daily swarming with a fresh supply of small mollusca and crustacea. Exactly the same laws will apply to mammals. Wild cats are prolific and have few enemies; why then are they never as abundant as rabbits? The only intelligible answer is that their supply of food is more precarious. It appears evident, therefore, that so long as a country remains physically unchanged, the numbers of its animal population cannot materially increase. If one species does so, some others requiring the same kind of food must diminish in proportion. The numbers that die annually must be immense; and as the individual existence of each animal depends upon itself, those that die must be the weakest—the very young, the aged, and the diseased,—while those that prolong their existence can only be the most perfect in health and vigour—those who are best able to obtain food regularly, and avoid their numerous enemies. It is, as we commenced by remarking, a "struggle for existence," in which the weakest and least perfectly organized must always succumb.[24]

[23] Wallace uses the passenger pigeon as an example of his point that abundance of offspring does not guarantee survival of a species, because living conditions ensure that few offspring survive to adulthood. His choice of example is ironic. In the nineteenth century, naturalists believed that the passenger pigeon was the most abundant bird in America. Their flocks were once up to a mile wide and three hundred miles long. However, as a result of hunting and agriculture, passenger pigeons were extinct by the early years of the twentieth century. Certainly the fact that they produced only one egg at a nesting was crucial to their demise.

[24] Wallace begins his essay with the statement that life for wild animals is a "struggle for existence," and he repeats

If now we have succeeded in establishing these two points — 1st, *that the animal population of a country is generally stationary, being kept down by a periodical deficiency of food, and other checks;* and, 2nd, *that the comparative abundance or scarcity of the individuals of the several species is entirely due to their organization and resulting habits, which, rendering it more difficult to procure a regular supply of food and to provide for their personal safety in some cases than in others, can only be balanced by a difference in the population which have to exist in a given area* — we shall be in a condition to proceed to the consideration of *varieties,* to which the preceding remarks have a direct and very important application.

Most or perhaps all the variations from the typical form of a species must have some definite effect, however slight, on the habits or capacities of the individuals. Even a change of colour might, by rendering them more or less distinguishable, affect their safety; a greater or less development of hair might modify their habits. More important changes, such as an increase in the power or dimensions of the limbs or any of the external organs, would more or less affect their mode of procuring food or the range of country which they inhabit. It is also evident that most changes would affect, either favourably or adversely, the powers of prolonging existence. An antelope with shorter or weaker legs must necessarily suffer more from the attacks of the feline carnivora; the passenger pigeon with less powerful wings would sooner or later be affected in its powers of procuring a regular supply of food; and in both cases the result must necessarily be a diminution of the population of the modified species. If, on the other hand, any species should produce a variety having slightly increased powers of preserving existence, that variety must inevitably in time acquire a superiority in numbers. These results must follow as surely as old age, intemperance, or scarcity of food produce an increased mortality. In both cases there may be many individual exceptions; but on the average the rule will invariably be found to hold good. All varieties will therefore fall into two classes — those which under the same conditions would never reach the population of the parent species, and those which would in time obtain and keep a numerical superiority. Now, let some alteration of physical conditions occur in the district — a long period of drought, a destruction of vegetation by locusts, the irruption of some new carnivorous animal seeking "pastures new" — any change in fact tending to render existence more difficult to the species in question, and tasking its utmost powers to avoid complete extermination; it is evident that, of all the individuals composing the species, those forming the least numerous and most feebly organized variety would suffer first, and, were the pressure severe, must soon become extinct. The same causes continuing in action, the parent species would next suffer, would gradually diminish in numbers, and with a recurrence of similar unfavourable conditions might also become extinct. The superior variety would then alone remain, and on a return to favourable circumstances would rapidly increase in numbers and occupy the place of the extinct species and variety.

The *variety* would now have replaced the *species,* of which it would be a more perfectly developed and more highly organized form. It would be in all respects better adapted to secure its safety, and to prolong its individual existence and that of the race. Such a variety *could not* return to the original form; for that form is an inferior one, and could never compete with it for existence. Granted, therefore, a "tendency" to reproduce the original type of the species, still the variety must ever remain preponderant in numbers, and under adverse physical conditions *again alone survive.* But this new, improved, and populous race might

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the line for emphasis at the end of this paragraph. With this phrase Wallace is anticipating a phrase coined by one of the most famous evolutionists of his day, Herbert Spencer, who first used the phrase "survival of the fittest" in *Principles of Biology* (1864).

Spencer began publishing his thoughts on evolution in *Social Statics* (1851), almost a decade before Darwin and Wallace put their views in print. Darwin credits Spencer with being influential in his thinking even though Spencer was primarily interested in social rather than biological evolution. Furthermore, whereas Darwin spoke of fitness in terms of reproductive success, Spencer used the term much as Wallace does here, to refer to those who were the strongest and healthiest.

itself, in course of time, give rise to new varieties, exhibiting several diverging modifications of form, any of which, tending to increase the facilities for preserving existence, must, by the same general law, in their turn become predominant. Here, then, we have *progression and continued divergence* deduced from the general laws which regulate the existence of animals in a state of nature, and from the undisputed fact that varieties do frequently occur.[25] It is not, however, contended that this result would be invariable; a change of physical conditions in the district might at times materially modify it, rendering the race which had been the most capable of supporting existence under the former conditions now the least so, and even causing the extinction of the newer and, for a time, superior race, while the old or parent species and its first inferior varieties continued to flourish. Variations in unimportant parts might also occur, having no perceptible effect on the life-preserving powers; and the varieties so furnished might run a course parallel with the parent species, either giving rise to further variations or returning to the former type. All we argue for is, that certain varieties have a tendency to maintain their existence longer than the original species, and this tendency must make itself felt; for though the doctrine of chances or averages can never be trusted to on a limited scale, yet, if applied to high numbers, the results come nearer to what theory demands, and, as we approach to an infinity of examples, become strictly accurate. Now the scale on which nature works is so vast—the numbers of individuals and periods of time with which she deals approach so near to infinity, that any cause, however slight, and however liable to be veiled and counteracted by accidental circumstances, must in the end produce its full legitimate results.

The hypothesis of Lamarck—that progressive changes in species have been produced by the attempts of animals to increase the development of their own organs, and thus modify their structure and habits—has been repeatedly and easily refuted by all writers on the subject of varieties and species, and it seems to have been considered that when this was done the whole question has been finally settled; but the view here developed renders such an hypothesis quite unnecessary, by showing that similar results must be produced by the action of principles constantly at work in nature. The powerful retractile talons of the falcon- and the cat-tribes have not been produced or increased by the volition of those animals; but among the different varieties which occurred in the earlier and less highly organized forms of these groups, *those always survived longest which had the greatest facilities for seizing their prey.* Neither did the giraffe acquire its long neck by desiring to reach the foliage of the more lofty shrubs, and constantly stretching its neck for the purpose, but because any varieties which occurred among its antitypes with a longer neck than usual *at once secured a fresh range of pasture over the same ground as their shorter-necked companions, and on the first scarcity of food were thereby enabled to outlive them.* Even the peculiar colors of many animals, especially insects, so closely resembling the soil or the leaves or the trunks on which they habitually reside, are explained on the same principle; for though in the course of ages varieties of many tints may have occurred, *yet those races having colours best adapted to concealment from their enemies would inevitably survive the longest.*[26] We

[25] The purpose of this paragraph is to describe the process of speciation from an ancestral population, but the general nineteenth-century belief that evolution was progressive resonates in Wallace's discussion of "superior" races and "inferior varieties," as well as in his insistence that new varieties are more "perfectly developed" than those they replace. Read on and you will see, however, that Wallace was clearly aware that a species achieved superiority only within a certain environmental context. Changing conditions could cause the extinction of previously well-adapted varieties.

[26] Jean Baptiste Lamarck (1744–1829) was an important naturalist and philosopher. In this passage, Wallace cites Lamarck's well-known example of giraffes acquiring long necks by stretching in order to refute Lamarck's notion of the inheritance of acquired characteristics. This idea, however, was only a portion of Lamarck's theory. Lamarck pro-

have also here an acting cause to account for that balance so often observed in nature,—a deficiency in one set of organs always being compensated by a increased development of some others—powerful wings accompanying weak feet, or great velocity making up for the absence of defensive weapons; for it has been shown that all varieties in which an unbalanced deficiency occurred could not long continue their existence. The action of this principle is exactly like that of the centrifugal governor of the steam engine, which checks and corrects any irregularities almost before they become evident; and in like manner no unbalanced deficiency in the animal kingdom can ever reach any conspicuous magnitude, because it would make itself felt at the very first step, by rendering existence difficult and extinction almost sure soon to follow.[27] An origin such as is here advocated will also agree with the peculiar character of the modifications of form and structure which obtain in organized beings—the many lines of divergence from a central type, the increasing efficiency and power of a particular organ through a succession of allied species, and the remarkable persistence of unimportant parts such as colour, texture of plumage and hair, form of horns or crests, through a series of species differing considerably in more essential characters. It also furnishes us with a reason for that "more specialized structure" which Professor Owen states to be a characteristic of recent compared with extinct forms, and which would evidently be the result of the progressive modification of any organ applied to a special purpose in the animal economy.[28]

We believe we have now shown that there is a tendency in nature to the continued progression of certain classes of *varieties* further and further

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posed that nature was animated by a universal tendency to perfection. All living things arose spontaneously and, over the course of history, evolved in the direction of increasing complexity. However, in addition to this general principal of perfection, Lamarck also argued that animals had to adapt to the rigors of their environment. It was through this sort of adaptation that animals acquired characteristics (like that long-necked giraffe) and passed them along to their offspring.

Lamarck's theory had a profound effect on the ideas of Darwin and Spencer. Both agreed with his notion of increasing complexity. Darwin and Wallace, in developing the theory of natural selection, rejected the inheritance of acquired characteristics. Spencer believed that in regard to social behavior, evolution was Lamarckian. Cultural traits were indeed acquired and passed on from generation to generation.

Lacking an adequate understanding of genetics, Darwin too eventually came to rely on acquired characteristics. In his 1868 work, *Variation of Plants and Animals Under Domestication,* Darwin proposed a theory he called pangenesis. He argued that characteristics acquired in life produced "pangenes" that could be carried by the bloodstream to the sex organs and hence transmitted to the next generation. Of course, this theory is no longer accepted.

[27] Wallace compares the action of evolution to the action of a governor on a steam engine. Many nineteenth-century authors compared the workings of evolution to the most advanced technology of their day. Spencer, in the next essay in this volume, invokes the telegraph as well as the railways. We continue to do this today. Since the mid-twentieth century, authors have commonly compared the workings of culture to computer hardware or software.

[28] Sir Richard Owen (1804–1892), a contemporary of Darwin, was a distinguished anatomist and paleontologist. Darwin attended his public lectures on comparative anatomy in 1837, and Owen described and catalogued for the British Museum the fossil vertebrates that Darwin collected during the voyage of the *Beagle*. Wallace is referring to some of Owen's work on vertebrate anatomy in this paragraph.

Owen was one of Darwin's professional associates for more than twenty years, but became a bitter opponent after the publication of *On the Origin of Species*. In his autobiography Darwin speculated that Owen was jealous of his success, but throughout his career Owen believed that life could not be reduced to material explanations. For example, based on his background in comparative anatomy Owen had reasoned that there was a common structural plan for all vertebrates that he called the "archetype." However, in Owen's thinking this archetype was not the ancestral form from which vertebrates are derived, but a model of the divine plan for vertebrates. Thus Owen's religious views prevented him from accepting Darwin's explanation for speciation and evolutionary change.

from the original type—a progression to which there appears no reason to assign any definite limits—and that the same principle which produces this result in a state of nature will also explain why domestic varieties have a tendency to revert to the original type. This progression, by minute steps, in various directions, but always checked and balanced by the necessary conditions, subject to which alone existence can be preserved, may, it is believed, be followed out so as to agree with all the phenomena presented by organized beings, their extinction and succession in past ages, and all the extraordinary modifications of form, instinct, and habits which they exhibit.

Ternate, February, 1858

NOTES

[a] This manuscript was never intended for publication, and therefore was not written with care.—C.D. 1858.

[b] I can see no more difficulty in this, than in the planter improving his varieties of the cotton plant.—C.D. 1858.