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## SPECIATION AND SELECTION

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THE splitting of one species into several descendant species was, for a long time, one of the most puzzling biological problems. Darwin was rather vague on the subject, in fact he did not even make a clear-cut distinction between evolutionary change within a species and the multiplication of species. The evolutionary modification of a species in the course of time ("phyletic evolution" of Simpson) and the splitting of a mother species into several daughter species are two separate, although closely related, problems. The latter phenomenon, namely the multiplication of species, is always meant in the following pages whenever the term speciation is used.

Even though by 1920 the basic laws of inheritance had been well established by the geneticists, Bateson, the founder of British genetics, was forced to admit ignorance concerning the process of speciation (Bateson, 1922):

When students of other sciences ask us what is now currently believed about the origin of species we have no clear answer to give. . . . That particular and essential bit of the theory of evolution which is concerned with the origin and nature of species remains utterly mysterious. . . . The production of an indubitably sterile hybrid from completely fertile parents, which have arisen under critical observation from a single common origin, is the event for which we wait.

We now know why Bateson and his contemporaries made no headway in elucidating the process of speciation. They were looking for the wrong thing because they had a mistaken species concept. Their thinking was unknowingly affected by a concept of idealistic philosophy. They were thinking of species as definite *types*, uniform within themselves, but separated from other species by an impressive morphological gap. The origin of such species would indeed be difficult to explain. It was this typological concept of species which induced de Vries to attribute the origin of new species to conspicuous major mutations. That this is not the solution of the species problem was, however, obvious to every naturalist.

The geneticists had found in the meantime that

there were considerable genetic differences between individuals of sexually reproducing species and that, true to Darwin's prediction, the various genotypes differed in their selective value. In fact, Haldane and Fisher had calculated that even very slight differences of selective value would affect the genetic composition of the respective populations in due time. Geneticists had also found that the source of this genetic variability was random mutation.

Paleontologists and taxonomists (and biogeographers), on the other hand, had shown that the evolution of a new species was usually an exceedingly slow process, requiring a minimum of several hundred thousand years and averaging perhaps a million years or more. Furthermore, they had shown that this process was a gradual one, yielding no evidence of jumps. *Natura non facit saltum*.

Selection within living populations is something nearly instantaneous, operating anew during each generation, while speciation requires for its completion a time interval equivalent roughly to 30,000 human generations. To explain one in terms of the other would seem an even more difficult methodological problem than to explain the evolution of stellar galaxies by events and forces within atoms.

How it was possible to connect the almost instantaneous event of selection with the infinitely slow process of speciation shall be the theme of my discussion. The problem was solved by an elucidation of the nature of the speciation process.

The first step was a revision of the species concept. The old "type concept" of the species was founded on a morphological species definition based on the degree of difference between species. For reasons that have been stated elsewhere (Mayr, 1942, 1948) this species concept was replaced by a biological species concept founded on distinctness, measured in terms of reproductive isolation. In this concept, a *species is a group of interbreeding natural populations that are reproductively isolated from other such groups*. The subjective criterion of the degree of morphological difference has here been replaced

by the objective one of reproductive isolation, a criterion which has the additional advantage of selective significance.

Further work showed that reproductive isolation alone is not sufficient to permit coexistence of two species at the same locality. They also must be sufficiently different in their ecological requirements to avoid too severe a competition (Crombie, 1947).

If one knows these two essential attributes of species it becomes much easier to define speciation. Speciation then means the evolution of reproductive isolation as well as of ecological differentiation between populations. It will be our task to investigate to what extent selection is involved in the evolution of these species requirements.

#### THE STRUCTURE OF SPECIES

Decisive proof for the course of speciation comes from a study of the structure of species. It can be shown that species are not the uniform, homogeneous "types" which the typologists made them out to be. Rather, each species is composed of a great number of more or less differentiated populations. The knowledge of the geographical variability of species has greatly helped our understanding of the process of speciation. Each local environment exerts a continuous selection pressure against these local populations, and molds them thereby into adaptedness. That most species are polytypic in regard to morphological characters has long been known to taxonomists. That such local populations differ also by numerous adaptive features of habits, ecology, and physiology, and that these features have a genetic basis is a much more recent discovery.

The pioneer work in this field was done by Goldschmidt who showed in a series of papers summarized in 1934 that many of the characters of the Gypsy Moth (*Lymantria dispar*) vary geographically, including such physiological attributes as rate of growth, size, pigmentation, and strength of the sex genes. The most obviously adaptive character studied by him is the length of the incubation period. During the winter the young larvae undergo a diapause and stay enclosed in the egg. Even if the diapause is broken artificially and the eggs are exposed to a constant warm temperature, there is a lag of a certain number of days before the larvae hatch. The length of this "incubation period" depends on a considerable number of factors, such as the experimental temperature and the length of the

preceding period of diapause. However, it is also closely correlated with the climatic characteristics of the place of origin of the eggs. In northern Europe and the northernmost island of Japan, where the vegetation develops very rapidly in spring after the long winter, the incubation period is short. In the Mediterranean, where the winters are warm but the vegetation is slow in spring, there is a very long incubation period, eighty-seven days at 11° C. against fifty-five days for central European eggs. The selective advantage of this accurate timing is obvious, since the larvae would die of starvation if induced by the warm winter weather of a Mediterranean country to hatch prior to the emergence of vegetation.

An impressive amount of similar evidence has accumulated since Goldschmidt's work confirming the thesis that each population of a species has been modified by selection to be adapted to the local environment. It would lead too far on this occasion to review this extensive literature covering both animals and plants. Only one more example shall be cited, the development of the Meadow Frog (*Rana pipiens*) (Moore, 1949). This species has a range that is much greater than that of any other North American frog, extending from Canada to Central America. There are pronounced climatic differences between various districts within this vast range, and this has led to the evolution of local populations which differ in their physiology. The most vulnerable period in the life cycle of these frogs is the embryonic stage between the fertilization of the egg and the metamorphosis of the young frog. It is in this stage that selection is most severe and it is in this stage that the greatest number of adaptive physiological differences between the various geographical races was found. Northern races (Quebec, Vermont, Wisconsin, New Jersey) and such from Louisiana tolerate a temperature low of 5° C. for normal development, while the lower limit is 9° for Ocala (Florida), 12.1° for Englewood (Florida), about 10° for Texas, and 12° for Mexico (Axtla). In turn, the southern populations were able to tolerate a higher temperature and still develop normally. The upper temperature limit for normal development in various populations was as follows: Quebec, Vermont, Wisconsin, and New Jersey 27.5°, Louisiana 32°, and Mexico (Axtla) 33°. At low temperatures northern frogs develop fast, e.g., at temperature 12° the number of hours required to reach embryological stage 20 (Moore,

1949) was as follows: Vermont 325, Louisiana 348, Florida (Ocala) 354, Florida (Englewood) 364, Texas 429, Mexico 396. There are additional adaptive differences in regard to egg size and shape of egg mass. It is evident from these data that the reason for the wide distribution of the meadow frog is its ability to become reconstructed genetically and to evolve genotypes that are adapted to the water conditions of the given region.

Numerous, usually much less well analyzed, examples of eco-geographical races in animals can be found in the literature (Mayr, 1942; Huxley, 1942).

#### NATURAL SELECTION IN LOCAL POPULATIONS

The simple fact that no two individuals (except identical twins) are alike in sexually reproducing species is too often ignored. One is willing to admit it for the human species and perhaps also for domestic animals, but all conspecific wild animals are commonly thought to be alike. To have proven that this is not the case is one of the major achievements of population genetics, foreshadowed by the population analysis undertaken by taxonomists. This variability includes not only the visible part of the genetic "spectrum," but also isoalleles and linked polygene systems. There appears to be an almost inexhaustible reservoir of gene combinations.

Even though much mortality in a population is due to accidents (rather than to lower fitness), there is unquestionably a greater probability that a superior (in selective qualities!) individual will reproduce than an inferior one. This will permit the rapid adaptation of a population to a local environment. It has been shown above that populations indeed are adapted to their local environment, but some more direct evidence shall be presented that this adaptation is due to selection.

#### NATURAL SELECTION UNDER EXPERIMENTAL CONDITIONS

As obvious as the effect of natural selection on adapted populations may be to the unprejudiced observer, irrefutable proof can be produced only by experiment. Such experiments proceed by two steps, both involving the raising of individuals from different natural populations under identical laboratory conditions. The first step consists in proving that indeed the two populations are genetically different by responding in a different manner to identical environmental con-

ditions. The second step consists in proving that survival is affected by these conditions. This would show that these conditions have selective value and can change the genetic composition of the population.

#### VARIOUS SELECTIVE FACTORS

As a selective agent the environment always acts as a whole. Sometimes it is possible to single out a specific factor and to indicate what role it plays in determining the genetic composition of a local population. Heuts (1947, 1948) has shown this for the effect of salt water and temperature on the Three-spined Stickleback (*Gasterosteus aculeatus*). In this species there are populations (type B) with a high number of plates on the sides of the body, which live mainly in coastal waters of high salinity, and inland populations (type A) with low plate number which live in fresh water. It was shown, as is to be expected, that in salt water there was a high percentage of hatching and survival of young of the salt-water race and low survival of individuals of the fresh-water race, while in fresh water the survival of the two races was reversed. Also there was very different survival of the different strains when raised at different temperatures.

The extensive work of Goldschmidt on *Lymantria dispar* has already been referred to above. It showed that numerous physiological characteristics of geographical races of this species have a genetic basis and in many cases it could be shown that larvae from different regions have different survival when raised under identical conditions. For additional evidence of differential survival of races of the same species see, among others, Speyer (1938), Basinger and Smith (1946), and Albonico (1948). What effect a particular factor has depends sometimes on a constellation of circumstances. Schüz (1942) showed for the White Stork (*Ciconia ciconia*) that the least mortality of young occurred in northwestern Germany during dry springs and in Hungary during wet springs.

Biotic factors of the environment are sometimes as efficient selective agents as climate or some other general factor of the environment. Armstrong (1945) showed that in a large, rather isolated pear orchard in southern Ontario a local race of the codling moth (*Carpocapsa pomonella*) had evolved which emerged two to three weeks later than the codling moth populations in apple orchards. This late emergence coincided with the softening of the ripening pears while young pears

have a stone layer under the epidermis which makes them impenetrable to these larvae.

Many species of insects are monophagous, that is they feed on a single species of host plant. The strong selective effect of the host plant becomes apparent when it is possible to shift individuals of such a monophagous species artificially to a new food plant. Chrysomelid beetles (*Gastroidea viridula*) that normally feed on sorrel (*Rumex*) had to be bred for two generations on knotweed (*Polygonum*) before they were adapted to the new food plant. During the first generation, while being submitted to forced feeding, nearly half the individuals died (*Kozhantshikov*, 1941). Adaptation to a specific food plant is obviously subject to severe selection.

One of the reasons why biotic factors often are such important selective agents is competition. Although the effect of competition had been postulated already by Darwin and was vaguely suspected ever since, it has been fully demonstrated only rather recently. If two closely related species of flour beetles, *Tribolium castaneum* and *T. confusum*, are brought together in a single homogeneous food medium, either one or the other species will be wiped out. *T. castaneum* usually becomes exterminated in cultures that are infected by the sporozoite *Adelina tribolii*, while *confusum* is usually the one that dies out in uninfected cultures (*Park*, 1948). In nature both species are widespread and prosperous, presumably because they are able to select slightly different niches and thus avoid fatal competition. It would seem superfluous to say anything more on the selective effects of competition since there is an excellent recent review on the subject (*Crombie*, 1947).

#### THE SEVERITY OF SELECTION

How quickly some genes respond to selection has been indicated in a number of recent papers although only part of the evidence is available in all these cases. The application of insecticides has resulted in an amazingly rapid evolution of highly resistant strains in many species of insects (*Quayle*, 1943). Very high selection coefficients have been made probable by *Goldschmidt* (1948) for the genes that produce industrial melanism in certain moths.

The new study of gene arrangements in *Drosophila* has the great advantage that genotypes are studied rather than phenotypes, although unfortunately it is unknown how many genes are situated on the inverted chromosome sections.

*Dobzhansky* (1947, 1948a, b) for *Drosophila pseudoobscura* and *Dubin* and co-workers for *D. funebris* (1946a, b) have shown that definite frequencies of certain gene arrangements have specific survival values. This became apparent from their distribution in nature and was corroborated by a study of experimental laboratory cultures.

#### CONCLUSIONS

Whenever and whatever tested, it has been shown that every population of a species is adapted to the conditions of the respective local environment. Furthermore, it has been shown that this adaptation is due to a balance of genetic factors which is often so delicate that it may respond to the seasonal and annual changes of the environment. Finally, these seasonal changes as well as the differences between populations are caused by selection.

The botanists have gathered an equally or even more impressive body of evidence in favor of these conclusions than the zoologists.

So overwhelming has the evidence become that these conclusions are not even denied by those, who, like *Goldschmidt* (1940), postulate evolution by large jumps, by macromutations or systemic mutations. The adaptation of local population and its causation by selection can be considered a fact.

#### THE BREAKING OF THE SPECIES BOND

If a species is as plastic as has been depicted, it is perhaps even more puzzling how it can split into several species. Perhaps a species is like a toy figure made of rubber which can be pulled into all sorts of shapes without losing its cohesion. This is indeed what *Goldschmidt* claims. According to him the local populations of a species are not incipient species. He believes that no amount of selective molding by the environment can change a population of a species into a new species.

To me it seems that all the available evidence indicates just the opposite. New species arise from isolated and much modified portions of parental species. The full evidence for this assertion has been given elsewhere (*Mayr*, 1942: 147-185). Only a summary can be given on this occasion. The most convincing proofs are these:

(1) The geographical subspecies studied by the taxonomist are often of the same kind as the

temporal subspecies studied by the paleontologist in successive strata. Since it has been possible in many cases to demonstrate the transformation of temporal subspecies into species, there is no reason to assume that geographical races should not do likewise if the circumstances are favorable.

(2) The distinctness of species is maintained by isolating mechanisms (Dobzhansky, 1941). To explain speciation it is necessary to explain the origin of these isolating mechanisms. If isolated populations of species are incipient species they also must have incipient isolating mechanisms. This indeed has been shown in an ever increasing number of cases. Frequently there is reduced fertility or almost complete sterility between geographically distant populations of the same species. Reduced fertility or partial ethological isolation has been found in many species of *Drosophila* and Lepidoptera (Mayr, 1948). Moore (1946) found much hybrid inviability between distant populations of the frog *Rana pipiens*. The voice, the courtship organs, and the structure of the genital armatures vary geographically in many species of animals. The Indian and European honey-bees (*Apis indica* and *A. mellifica*) are reported not to be crossable even though linked by a series of intergrading populations (Goetze and Schmidt, 1942). A similar geographical variability is shown by habitat preference, food plant preference, season of reproduction, and all the many other factors of which isolating mechanisms are composed. The picture presented by the geographical variation of isolating mechanisms is fully consistent with the theory of geographical speciation.

(3) There is hardly a genus of animals which does not contain some incipient species or borderline cases. In many species, there are isolated, peripheral populations that are so distinct that they could be classified with equal justification as species or subspecies. There are the so-called superspecies, groups of allopatric species, which reveal through their distribution pattern that they are the products of geographical speciation. There are the multiple invasions of islands which prove that during isolation a population can reach species level. Finally, there is an ever increasing number of rings of races known in which the terminal links overlap without interbreeding while there is complete interbreeding between the adjacent populations of which the ring is composed. The existing number of such borderline cases is far in excess of the number needed to replace those species that appear to be vanishing.

More convincing proof for geographic speciation can hardly be expected.

#### SELECTION AFTER SECONDARY OVERLAP

Selection not only starts speciation by causing genetic divergence of originally similar populations, selection also completes speciation. Species require two attributes in order to coexist successfully side by side, reproductive isolation and ecological compatibility. These attributes are acquired by isolated populations only incidentally, namely as by-products of the general genetic divergence occurring during isolation.

When such populations come together again secondarily, any one of three things may happen. Either they have not acquired reproductive isolation, then the formation of a "hybrid" zone will occur, or else they have acquired reproductive isolation but not ecological compatibility. The result will be a meeting of the two species along a sharply defined border without any noticeable overlap.

Finally, they may acquire both prerequisites and if this condition is fulfilled the last obstacle is removed from a wide mutual overlapping of their ranges. However, since both species are not "types" in the sense of the natural philosophers but variable populations, they may and usually will contain individuals that are either not completely reproductively isolated or not completely compatible ecologically. Here again selection sets in. The ecologically incompatible individuals will be at an obvious disadvantage. This is equally true for individuals that are not reproductively isolated for they will produce hybrids, and hybrids are nearly always of lower fitness and their genes will be eliminated. The result will be greater survival of the individuals with well developed isolating mechanisms and hence a steady improvement of these mechanisms. There is some evidence that this is not pure theory. Dobzhansky (1941) found that there was a greater amount of isolation between *Drosophila miranda* on one hand and both *D. persimilis* and *D. pseudoobscura* if populations of the latter two species were used that came from the area of overlap. King (1947) found that among three very closely related species of *Drosophila*, the two species which occurred sympatrically in Brazil, *D. guarú* and *D. guarani*, were completely isolated sexually. The two species, however, interbred fairly freely with an allopatric third species, *D. subbadia*, which is known only from Mexico. An improvement of isolating mechanisms in

zones of overlap was also found in *Triturus* (Lantz, 1947).

Evidence for the selective effect of competition on ecological species differences has been presented by Lack (1947) for the Galapagos Finches and by Amadon (1947) for the birds of the Hawaiian Islands.

#### SUMMARY

Geographical speciation is the normal process by which species multiply. Isolating mechanisms are formed as a consequence of the genetic divergence of populations, while they are protected by extrinsic barriers against disturbing gene flow from other populations of the parental species.

Natural selection is effective at three stages of the speciation process,

(1) it continually molds all the populations of a species to be adapted to their local environment,

(2) it remodels isolated portions of a species while they are protected against gene flow from the main body of the species,

(3) it perfects isolating mechanisms after the two populations have reestablished contact and eliminates individuals with imperfect isolating mechanisms. Likewise, it tends to eliminate individuals that are closest to other sympatric species in their ecological requirements.

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