

# ECOLOGICAL FACTORS IN SPECIATION

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The past decades have seen the gradual formulation of the theory of geographical speciation, principally based on work in the fields of the systematics of mammals, birds, insects, and mollusks. This theory postulates that in bisexual animals a new species can develop only "if a population, which has become geographically isolated from its parental species, acquires during this period of isolation characters which promote or guarantee reproductive isolation when 'the external barriers break down'" (Mayr, 1942). A number of workers in recent years have considered this statement an oversimplification. The omission of any reference in this description of the speciation process to the ecological factors—so vitally involved in the process of speciation—has also been objected to. Even though the importance of geographical speciation is universally admitted, there are a number of authors, particularly among the ichthyologists and entomologists, who believe that in addition to geographical speciation there is another process of speciation, variously referred to as ecological or sympatric speciation. Thorpe (1945), for example, is inclined to consider that in addition to geographical speciation there is a speciation process which is characterized by the fact "that local differences of habit may be the starting point for the evolution of new species."

It appears to me that there is no real conflict between those authors who stress the ecological aspects of speciation, such as Stresemann (1943) and Thorpe (1945), and those who, like myself, have stressed the geographical aspects. This was pointed out by Timofeeff-Ressovsky

(1943). The seeming differences are due partly to misunderstandings and partly to a different emphasis placed on various aspects of a single process of speciation. The field has suffered from looseness of thought and vagueness of expression, and it may therefore be useful to attempt a fresh analysis and possibly a synthesis of the two viewpoints. The principal obstacle blocking such synthesis up to now has been that those authors who have emphasized the role of ecological factors in speciation generally accept sympatric speciation as an integral part of ecological speciation. To remove this difficulty, a special section (pp. 269–285) has been devoted to a discussion of sympatric speciation. It is more important, however, to determine the respective roles of geographical and ecological factors in speciation, and to find out whether they operate consecutively or concomitantly.

The field has suffered particularly from the lack of a clear-cut *Fragestellung*. The result has been that only few investigations have ever been undertaken which would give decisive answers to the unsolved questions. Most of the published studies sadly miss the crucial points. It is one additional object of this discussion to focus the attention of investigators on those aspects that are in particular need of further study.

## I. THE PROCESS OF SPECIATION AND THE ROLE OF ECOLOGICAL FACTORS

The most important aspect of speciation is that it is a process involving populations rather than individuals—contrary to the views of De Vries and other early Mendelians. The gene pool of a whole

population serves as "the material basis of evolution," which is so often referred to in the genetic literature. The problem of speciation then boils down to two questions:

- (1) *How do new populations<sup>1</sup> within a species develop?*
- (2) *How do such populations become reproductively isolated from other populations of the parental species?*

Two steps are thus involved in speciation, (1) the establishment of new populations and (2) the establishment of intrinsic reproductive isolation. Geographic speciation assumes that, as stated, the sequence of these steps is 1-2. Sympatric speciation assumes that the first step is the origin of reproductively isolated individuals which subsequently establish a new species population. This is a logically consistent hypothesis since two separate sympatric populations cannot exist unless they are reproductively isolated. The objections to this sympatric speciation hypothesis will be fully stated in the second section. But, first an attempt shall be made to answer the following questions: How does the theory of geographic speciation explain the origin of new populations and of reproductive isolation between them? How does it evaluate the role of ecological factors in these processes? Furthermore, what is understood when the expression "geographically isolated" is used?

#### *What is Geographical Isolation?*

When two populations are separated by such a formidable barrier as a vast desert, or an ocean, or an extensive, high mountain range, everyone will agree that they are geographically isolated. However, is a corn field geographically isolated from

the next corn field by an intervening wheat field? How large must the distance be between "isolated" populations? How much gene flow is permissible?

Unfortunately, no general answer can be given to these questions. It depends on the circumstances of each case. The less suitable a given habitat is for a species, the more efficient a barrier it becomes. The term "geographically isolated" is to be construed broadly and refers to any environmental factor that effectively inhibits gene flow between two neighboring populations. In addition to the macrogeographical isolation of the above listed geographical barriers, there are many cases of *microgeographical isolation* where no great distances nor conspicuous barriers are involved. The terms topographical or spatial isolation have often been used for these situations, particularly in the case of species with short average cruising range, such as are typical for many invertebrates. However, opposing the terms geographical and spatial isolation creates the erroneous impression that two different principles are involved. This is not the case. Whether large or small distances are involved, in all these instances there is a stretch of unsuitable terrain which inhibits dispersal and thus reduces gene flow. The term "microgeographical isolation" is thus preferable to "spatial" or "topographical" isolation.

All the terminologies so far proposed break down in those cases where two populations that differ in their ecological requirements are in contact but do not overlap. Are they species or subspecies? Should they be called sympatric or allopatric? In the narrowest sense, they are, of course, allopatric but, carrying the argument to the limit of absurdity, are not any two individuals allopatric? The terms sympatric and allopatric have been very useful in focussing attention on the spatial relationship of natural populations, but they seem to become meaningless in those cases where ecologically different populations exclude each other in space.

<sup>1</sup> A population is a group of freely interbreeding individuals of a locality. Separate sympatric populations belong, by definition, to different species. Separate conspecific populations must, also by definition, be allopatric during their breeding season (except in the rare cases of seasonal separation in zones of secondary overlap).

If a meadow and a forest species occur in the same general region, are they allopatric or sympatric? This problem is particularly acute where habitats occur as widespread features of the landscape, sharply delimited against each other, such as is frequently found in the tropics and subtropics or wherever the original landscape has not yet been disturbed too severely by man. Here, differences in ecology are also such of geography. The reality of this problem is evident to every naturalist.

In a recent letter Mr. R. E. Moreau wrote me about the following situations concerning African birds. "In each of the mountains of East Africa a mountain forest white-eye (*Zosterops*) is found which is isolated as completely from the other montane ones as if it inhabited an oceanic island. I doubt whether any one of them comes into regular contact with the non-forest species (*Z. senegalensis*) which entirely surrounds them geographically but seems to avoid the immediate neighborhood of forest patches. An even more critical example of this sort of thing is provided by the two drongos, *Dicrurus ludwigii* and *D. adsimilis*. The former, in my experience, never ventures outside the edge of the evergreen forest, the latter seems never to perch even on the outside edge of a forest tree. Yet, both may occur within 50 yards of each other and the latter species is quick to occupy a clearing made in evergreen forest. I have come across some other nice examples, such as where *Cossypha heuglini* and *C. semirufa* occur in the same locality. The former is always restricted to its normal habitat, namely, bush country outside the forest, while the latter is found only in the forest. In one or two mountain forests where *C. semirufa* is absent the other bird replaces it. Are these species sympatric or allopatric?"

A universally applicable answer cannot be given to all the above questions. They must be answered from case to case and the answer inevitably will depend on the circumstances.

#### The Invasion of New Habitats

The process of speciation results in ecological diversification and consequently in an ever-increasing efficiency in the utilization of the environment (Mayr, 1948b; Lack, 1948). One aspect of gradual speciation is therefore that it is an ecological process. Every species lives on an adaptive peak and the problem of speciation is how to reach new, not previously occupied, adaptive peaks. A species might do this either (1) by becoming locally more euryoecous (ecologically tolerant) or (2) by invading new areas with different ecological conditions. As far as the first possibility is concerned, a population that was previously restricted to the forest might become adapted to live in orchards or meadows as well as in the forest. Observations show that this occurs only very rarely. A species that is adapted for life in the forest will normally not be able to survive the competition it meets in the meadow. A population adapted to live on one species of food plant will normally not be able to enlarge its niche to include a second kind of food plant, unless its genetic make-up is altered. To be sure, individuals of many species try continuously to invade new niches. Such colonizations are often temporarily successful, but a single adverse season usually reduces the ecological amplitude of the species to its normal width. Some species are, at least locally, restricted to an extremely narrow niche, others are more tolerant in their ecological requirements. Whether its niche will be broad or narrow is largely a function of the genetic constitution of the respective population. A local gene complex can become modified by the usual genetic processes so as to increase or decrease the ecological tolerance of the population of which it is the genetic basis, but the development and simultaneous maintenance in the same area of two different gene complexes adapted for two different ecological niches will be prevented by gene flow. Some especially successful

species, the euryoecous species of the ecologist, get around this difficulty by developing a gene complex that is equally satisfactory in a number of different habitats. Such species are; however, rather rare.

How then does a species colonize a new type of habitat? A glance at the distribution map of ecologically variable species gives us a clue. The ecologically (as well as genetically) most aberrant populations are nearly always found along the periphery of the range of the species. This has several separate reasons. One of them is that the one-directional gene flow near the border of the range increases the rate of evolutionary change, another is that the normal habitat in the center of the range may not offer optimal living conditions near the periphery, a situation that encourages a shift in habitat. Many specialized species have been able to develop in each district a geographical race adapted for the locally most abundant or otherwise most satisfactory ecological niche. The Red Crossbill (*Loxia curvirostra*) offers a particularly graphic illustration of this important principle (Kirikov, 1940). The mountains of central Asia (Himalayas, Altai) were probably the original home of the species. It lives there on the prevailing coniferous trees, various species of spruce (*Picea*) or larch (*Larix*), and has developed a rather thin, slender bill. From here the crossbill has spread east and west and has reached a number of areas where pines (*Pinus* spec.) are the prevailing or exclusive tree, such as in the Crimea (*L. c. mariae*), in Tunisia (*L. c. polyogyna*), in the Balearic Islands (*L. c. balearica*), and particularly in northern Europe (*L. c. pityopsittacus*), also in the southwestern United States and Central America. In these areas geographical races of the crossbill have developed which have large, heavy bills adapted to the opening of the tough pine cones. However, only one race has developed in the areas where there are two prevalent conifers, such as *Pinus cembra* and *Picea excelsa* in the Alps. The Cross-

bill of the Alps (*L. c. curvirostra*) is a spruce race. The only apparent exception occurs in parts of northern Europe where the "subspecies" *curvirostra* and *pityopsittacus* are reported to breed in certain districts side by side without mixing. The greater portion of the ranges of these two forms is, of course, still separate, revealing their geographical origin. The evidence indicates that the most distinct of these "ecological" races originated in complete geographical isolation. This is, of course, even more true for the "ecological" races among the Galapagos Finches (Lack, 1947) and Hawaiian Honeycreepers (Amadon, 1947).

At first sight the concept of a geographically and ecologically variable species seems full of contradictions. We see that in one locality a species is restricted to a very definite habitat niche, while in another locality it occurs in a different, sometimes very different, niche. We know that through selection in each of these populations a definite gene complex has developed, which permits the population to survive and thrive in spite of competition, predation, and all sorts of other adversities. I had asserted in 1942 (p. 196) that geographical isolation precedes the formation of ecological preferences in every case. If this were true how could species ever invade new habitats, as they undoubtedly do? Thorpe (1945) correctly points out this contradiction.

There is thus great need for studies by experiment and observation under what conditions individuals of a species can shift to new habitats and become the progenitors of new populations. Unfortunately, the evidence is scanty and has been interpreted in various ways. It is this aspect of the speciation problem that has been given special attention by Thorpe.

The adaptation for life in a given habitat includes the faculty of the individual of the species to select this habitat (from a vast array of other possible ones!) during the dispersal phase. Although genetic

factors must to some extent control this ability of habitat selection, nevertheless it is not entirely rigid and undeviating. There is a certain amount of ecological plasticity which is greater in some species, less in others.

The establishment of individuals in a new environment will be assisted by conditioning, as emphasized by Thorpe (1945); as well as by "organic selection," that is, the gradual substitution of modifications by mutations (Baldwin, 1902; Gause, 1947). A new population within the species will thus come into being and will permit the species to spread into areas that were previously outside the breeding range. It is probable that most range expansions of species are caused by the origin of such new intraspecific populations. This is well illustrated by the recent spread of the Mistle Thrush (*Turdus viscivorus*) in northwestern Europe (Peitzmeier, 1942). This species had lived for a long time in the coniferous mountains south of Westphalia, but did not invade the lowlands until 1928. By 1939 it was common in the deciduous woods and farm gardens of the area, a habitat strikingly different from the pine and spruce forest of the nearby mountains. Peitzmeier, in tracing this invasion back to its source, presents evidence which shows that it did not come from the neighboring mountains but rather from the west (northern France, Belgium) where the Mistle Thrush had always been an inhabitant of deciduous lowland woods and gardens. From here it spread eastward through Holland and across the Rhine into Westphalia. Thus the invasion of the deciduous woods of Westphalia is not due to a shift in the tolerance of the population from the coniferous woods of the hills around Westphalia, but due to the range expansion of an already existing deciduous woods population. Unfortunately, nothing is known as to the relationship of the two populations, but it is quite possible that at the present time there is very little gene exchange between these two geographical-ecological

races of the Mistle Thrush. It would be interesting to determine through banding whether there is any interbreeding in the zone of contact. It would also seem important to determine where and how the deciduous woods population of northern France had originated.

Not always are the ecological differences as clearly associated with geographical features (different distributions) as in the case of the Mistle Thrush. The smaller the normal cruising range of individuals of a species, the smaller becomes the geographical range of a local population, and the more difficult it is to discern that the establishment of new populations is a microgeographical phenomenon rather than a purely ecological one. The literature of economic entomology is replete with cases of locally segregated populations showing ecological differences. The Codling Moth (*Carpocapsa pomonella*) is particularly apt to develop such local races. Armstrong (1946) recently described a local population of this species from the Province of Ontario (Canada) which had developed in a large, eighty-year old pear orchard, which "is more or less isolated from other large pear or apple orchards." While moths in Ontario apple orchards have their peak of emergence between June 26 and July 17, the moths in this pear orchard emerged mainly between July 17 and August 7, thus two weeks later. The delayed emergence of the pear moths coincided with the period during which the pears softened and became penetrable for the larvae. Armstrong points out that only "the absence of large apple orchards in the vicinity has prevented this strain from being swamped by crossing with the generally prevailing apple strain." For, even though the peaks and extremes of the emergence curves are well separated, there is still a large area of overlap of emergence time which would result in rapid swamping if it was not for the geographical segregation.

Several other populations of the apple codling moth are known that have in-

vaded other hosts and have developed partly microgeographically-segregated and biologically-distinct populations. In California and in other areas the codling moth attacks the walnut. The first damage to walnut crops in California was reported in 1909. The first heavy infestation was in 1931 although apples and pears had been heavily infested in nearby districts since 1880 (Boyce, 1935).

This interesting case has never been analyzed fully. It is not known whether there are two separate strains of the codling moth in the walnut districts or whether the ecological requirements of the local race have become broader, permitting life both on apple and walnut. There is comparatively little apple growing in the chief walnut districts, and it appears possible that the codling moth population in the walnut districts has changed completely into a "walnut strain." It would be intensely interesting to follow up these possibilities. All we know up to now is that an evolutionary change has occurred in the apple codling moth of the walnut-growing districts of California, since it has invaded a new host fifty years after its introduction into California. The existence of such cases is not necessarily proof for sympatric speciation since, as stated, there are several alternative possibilities.

#### *Amount of Gene Flow Between Incipient Species*

All geographical barriers are relative. Even the most isolated islands are frequently visited by strays from the nearest mainland. Hundreds of continental species of animals are annually recorded from Great Britain. The interruption of gene flow even between two "isolated" populations is thus always relative and incomplete (figure 1B). If two such populations diverge nevertheless, it proves that the combined effects, of mutation pressure, selection, and random fixation (+ recombination) outweigh the equalizing effects of gene flow.

This leads to the simple, but important,

question: How strong must the gene flow be to prevent the genetic drifting apart of two populations? It is very unlikely that the purely genetic processes of mutation pressure and random fixation cause changes of a sufficiently high order of magnitude to hold any sizable gene flow in check. It may be different with selection pressure, but unfortunately it has never been determined how much gene flow strong selection pressure can neutralize.

Let us consider, for example, two spatially segregated, contiguous populations within a species which are not separated by an extrinsic barrier. Selection pressure will tend to pull these two populations apart, if they live in rather different habitats. But, can selection overcome the effects of dispersal across the zone of contact? Can conditioning reduce dispersal across the line of contact to such an extent that it no longer prevents the steady divergence of this population? Sufficient facts are not available for a decisive answer to these questions. The scanty evidence that is available indicates that speciation by geographical segregation (without isolation) is rare, if it occurs at all. Ecological differences are rarely abrupt in zones of primary intergradation. There is likely to be an intermediate habitat with an intermediate population to serve as a channel for the gene flow. In the cases where two ecologically very different subspecies are found in immediate contact, it can nearly always be shown that secondary contact is involved.

The only study known to me of the effect of gene flow across a habitat border is an investigation by Blair (1947) of the deer mouse (*Peromyscus maniculatus*) populations on pinkish gray and dark red soils in the Tularosa Basin. Populations that occur eighteen miles apart on differently colored soils show adaptive differentiation in the frequency of buff and gray genes. However, there was no difference between the populations found in two stations on different soils only four miles apart. Future investigations must

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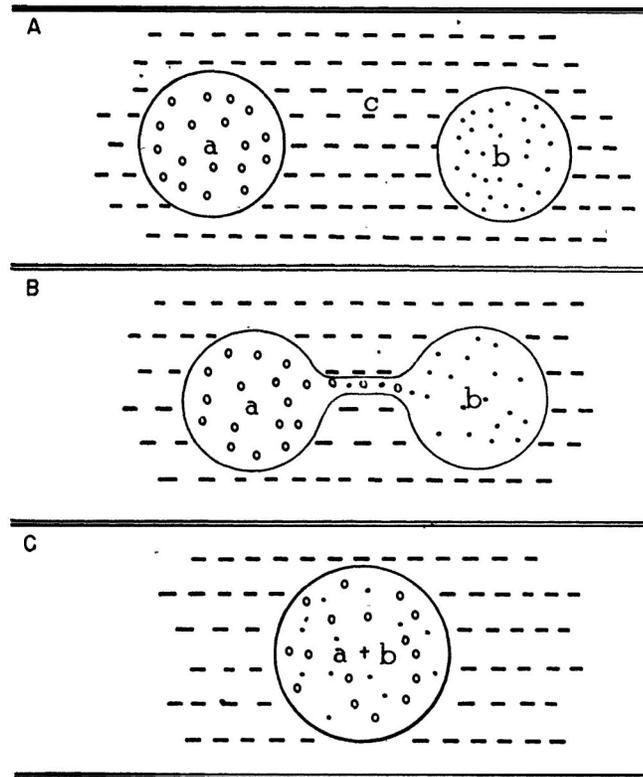


FIG. 1. Spatial relationship of two populations *a* and *b* (diagrammatic). A. Completely isolated by unsuitable terrain. B. Incompletely isolated; some gene exchange through partial barrier. C. Completely sympatric, but partially or completely segregated in different ecological niches.

show to what extent a stronger habitat preference can reduce the width of the dispersal belt.

It is unfortunate that so little evidence is available on this problem. Sympatric speciation would appear more probable if speciation by geographic segregation was at all common. It is here that the chief difference of opinion seems to exist between those who believe in occasional sympatric speciation and those who do not. The adherents of sympatric speciation believe that invasions of new—geographically not isolated—habitats are sufficiently irreversible and conditioning for these new habitats sufficiently complete to prevent dispersal and permit the building up of distinct gene complexes. A thorough examination of the whole problem of sympatric speciation is therefore essential for the proper evaluation of the various possibilities.

## II. AN ANALYSIS OF SYMPATRIC SPECIATION

The role of ecological factors in geographic speciation was discussed in the preceding section. The present section shall be devoted to answering the question whether or not there is a separate process of sympatric speciation, independent of geographic speciation. What "sympatric speciation" is has never been properly defined, but it is generally characterized by one or both of the following assumptions: (a) the establishment of new populations in different ecological niches within the normal cruising range of the individuals of the parental population (figure 1C), (b) the reproductive isolation of the founders of the new population from individuals of the parental population. Gene flow between daughter and parental populations is inhibited by in-

trinsic rather than extrinsic factors. A rapid, if not almost instantaneous, process of species formation is implied in most schemes of sympatric speciation.

*Historical.* The concept of sympatric speciation goes back to pre-Darwinian days. Darwin himself was uncertain about this question as is evident from his correspondence with Wagner, Semper, and Weismann, and as indicated in numerous passages in his works, e.g.:

"If a variety were to flourish so as to exceed in numbers the parent species, it would then rank as the species, and the species as the variety; or both might co-exist, and both rank as independent species."

"The small differences distinguishing varieties of the same species, steadily tend to increase till they come to equal the greater differences between species of the same genus, or even of distinct genera."

Darwin makes no distinction between speciation through individuals (individual varieties) and speciation through populations (subspecies). While in some of his statements he seems to place due weight on the geographical element, in others he seems to ignore it altogether. It was, M. Wagner who, in a series of papers from 1868 to 1889, brought out the importance of geographical isolation of populations for the multiplication of species. At first these ideas found few adherents, radical and novel as they were. On the contrary, the last two decades of the nineteenth century witnessed the greatest flowering of the concept of sympatric speciation. Romanes devoted an entire volume of his book *Darwin and after Darwin* (1897) to a theory of sympatric speciation which he called the theory of physiological selection. He and his followers insisted that geographical speciation was only of minor importance for the origin of new species. The argument of this school is based on two concepts, one unproven and very unlikely (that of homogamy), and the other definitely wrong (that of blending inheritance). Since they took blending inheritance for granted, they had to postulate the existence of homogamy (see also Pearson,

1900). The concept of homogamy or associative mating states that within a population the most similar individuals will mate with each other. For "so long as there is free intercrossing, heredity cancels variability, and makes in favour of fixity of type. Only when assisted by some form of discriminate isolation [= preferential mating], which determines the exclusive breeding of like with like, can heredity make in favour of change of type, or lead to what we understand by organic evolution" (Romanes). The most significant point of this argument is that new populations are formed by the non-random mating of individuals within populations. Romanes' theory is merely an elaboration of the theories first independently proposed by Catchpool (1884) and by Dahl (1889). All these theories have three postulates in common (which shall be discussed below): homogamy, complete linkage of mate selection and habitat selection, and the absence of genetic segregation.

The confused reasoning of this school cannot be illustrated better than by the following quotation:

"Suppose that on the same oceanic island the original colony has begun to segregate into secondary groups under the influence of natural selection, sexual selection, physiological selection, or any of the other forms of isolation, there will be as many lines of divergent evolution going on at the same time (and here on the same area) as there are forms of isolation affecting the oceanic colony" (Romanes, 1897). Actually, of course, exactly the opposite is true. Isolated oceanic islands are exemplary for monotypic evolution as Lack (1947) has demonstrated so convincingly in connection with the Cocos Island Finch.

It would be foolish to quote these fallacies if it were not for the fact that the very same arguments are still used today to endorse sympatric speciation. The only novel feature is that nowadays the occurrence of "macromutations" is sometimes postulated, as for example by Valentine (1945): "Speciation may proceed

within a population as a result of the appearance of relatively drastic changes (mutations) that are recognized by both the mutants and the norms, causing reluctance to cross. This, in brief, is the principle of associative speciation."

*The Evidence for Sympatric Speciation*

There must be some reasons why there are still so many authors left who believe that a process of sympatric speciation occurs in addition to allopatric (geographical) speciation. Botanists, in particular, have frequently stated that they find relatively little evidence for geographical speciation. Romanes (1897) quotes Nägeli to the effect "that in the vegetable kingdom closely allied species are most frequently found in intimate association with one another, not, that is to say, in any way isolated by means of physical barriers." In fact, all of the cases quoted by Romanes as proving sympatric speciation are taken from the plant kingdom. As is now known, instantaneous sympatric speciation through polyploidy is actually a common occurrence among plants. Apomixis, hybrid swarms, and the polytopic formation of ecotypes further complicate the picture. On the other hand, speciation in sexually reproducing plants seems not to differ materially from speciation among sexually reproducing animals.

Two classes of phenomena are frequently quoted as proving the existence of sympatric speciation. One consists of experiments showing that parasitic insects, as well as monophagous or oligophagous food specialists among plant feeders, can be conditioned to accept new hosts. The other is the occurrence of "species swarms" among freshwater organisms in many reputedly rather recent lakes where, it is believed, geographic speciation could not have been operating. The significance of this evidence shall be discussed below.

The main reason for postulating sympatric speciation, however, seems to be the fact that invariably there are ecological

differences between closely related and morphologically similar sympatric species. This ecological specialization leads to a wonderfully efficient way in which the numerous species of a locality utilize their environment. It is argued that such perfect adaptation could not have developed in geographical segregation. There is a strong reluctance among naturalists against admitting the evolutionary role of accident. Just as the Lamarckian finds it impossible to believe that the wonderful morphological adaptations found in nature could be the result of random mutation and selection, in a parallel manner some ecologists find it hard to accept that ecological speciation should happen in the apparently round-about way of spatial segregation rather than by the direct route of sympatric habitat choice.

*Assumptions Underlying the Concept of Sympatric Speciation*

The thesis of sympatric speciation cannot be discussed profitably before some of the assumptions are stated more succinctly than are made by the adherents of this thesis. Two recent papers contain a clear statement of the major assumptions. Thorpe (1945) visualizes the following procedure of sympatric speciation:

"Imagine now an area where two types of habitat 'a' and 'b' (e.g. two different vegetational types) are available in mosaic distribution and a species (of bird) confined to habitat 'a' within that area. In some exceptional circumstances of crisis or as a result of some slight germinal change certain individuals of the species spread into habitat 'b' and the young reared there become imprinted, or otherwise specialized, to the new niche. If this niche provides room for expansion, the birds of the new habitat will rapidly come to fill it during which time they will be reproductively isolated to a considerable extent from the 'a' habitat birds."

In this scheme Thorpe implies thus the assumptions (1) that young birds raised in a new habitat will "become imprinted, or otherwise specialized, to the new niche" to such a degree that they will not reenter the ancestral habitat to any appreciable extent, but rather establish at once a new

population by a more or less irreversible process. (2) That such individuals "will be reproductively isolated to a considerable extent" from the inhabitants of the ancestral habitat by being completely restricted to the new habitat. The choice of habitat and not microgeographical segregation would be the isolating factor since the two habitats are "available in mosaic distribution" (see figure 1C).

Test (1946) considers sympatric speciation as a preadaptation process. "Ecological speciation is that differentiation which has taken place during isolation of extreme variants which could not survive in the parental microhabitat, but which are able to take over a microhabitat not compatible with the parental morphology and ecology. This isolation is not of a geographic type, but is due to the unsuitability for the parent stock of the microhabitat invaded by the offshoot." In connection with this hypothesis the following assumptions are made explicitly or by implication:

(1) That new species may be established by extreme individuals rather than by populations.

(2) That such founders and their offspring are different genetically from the parent population.

(3) That such founders are preadapted for a habitat different from the parental habitat.

(4) That—in order to survive—such individuals search for the habitat for which they are preadapted.

(5) That during the original colonization "an intervening area" can be crossed which later no longer can "be crossed by individuals of either stock."

Each of these assumptions is arbitrary and largely unsupported by facts. Combining several of these improbable assumptions into a single hypothesis increases their improbability.

#### *Objections to the Hypothesis of Sympatric Speciation*

Every one of the various proposed hypothetical models of sympatric speci-

ation makes certain unproven assumptions. Obviously, even if all these assumptions should turn out to be invalid, it would not necessarily prove that the basic hypothesis is wrong. In any case, a critical evaluation of the various assumptions will lead to a clearer understanding of the problem.

(a) *Homogamy*. The concept of homogamy states that within a population the most similar individuals will prefer to mate with each other. The postulation of homogamy was the inevitable consequence of the theory of blending inheritance because random mating would soon lead to a complete elimination of genetic variability in a population under the theory of blending inheritance. Dahl (1889), Romanes (1897), Pearson (1900), and many other writers of that period who were unaware of the prevalence of geographical speciation, claimed that homogamy was an indispensable requisite of speciation. However, positive evidence for the occurrence of non-random mating within populations is exceedingly meager. Exceptions are provided by species that are very variable in size and continue to grow after reaching maturity. In the nudibranch *Chromadoris zebra*, for example, Crozier (1918) found that courtship usually broke off between individuals of too uneven size and that there was considerable correlation (about 0.6) between the sizes of the sexes in copulating pairs. However, in this and other similar cases there was complete overlapping between neighboring size classes and no evidence for the origin of any discontinuities owing to this associative mating. Furthermore, in many other less variable species (Alpatov, 1925; Spett, 1929) there was no correlation in size between copulating individuals. As far as color characters or other species characters are concerned, the evidence is even more completely negative. Among the numerous cases of polymorphic vertebrates that have been investigated the only known case of probable non-random mating is that of the Snow Goose-Blue Goose (Manning,

1942). Of the 1500 Blue Geese that were nesting on Southampton Island among about 30,000 Snow Geese, 850 formed pure Blue pairs instead of about 180 as would be expected on the basis of random pairing. Unfortunately, these raw data are inconclusive since the distribution in subcolonies was not investigated, and the geese are well known to form small clans. Nor were the heterozygotes taken into consideration in these calculations. Koss-wig (1947) suggested recently that homogamy might explain the rapid speciation of cichlid fishes in the East African lakes. Not only does he produce no evidence to support this speculation, but he is definitely in error when he believes that monogamy will necessarily result in homogamy. Gershenson (1941) has been able to prove conclusively that there is random mating among the color phases of the hamster (*Cricetus cricetus*). The same has been shown for color patterns in insects (Spett, 1929). The only apparent exception is the yellow mutant in *Drosophila melanogaster* and probably in other species of the genus (Spett, 1931; Diederich, 1941). However, in this case there is only partial one-directional mating preference and the viability of individuals of this mutant is so inferior to wild type that it would be rapidly eliminated in wild populations. Even where there is a slight amount of homogamy, its role in speciation can apparently be neglected, for Hogben (1946) states (p. 163) on the basis of extensive calculations: "Positive assortative mating can have very little importance as an evolutionary process unless it is exceedingly intense." This discussion can then be summarized in the statement that evidence in favor of homogamy is virtually nonexistent and that homogamy, where it exists, is not of the type that would lead to the establishment of discontinuities within populations.

(b) Linkage of mate preference and habitat preference. Romanes and others seem to take it for granted that if a species is found at a given locality in several

niches, mating occurs only between those individuals that live in the same ecological niche. The choice of a new niche would then automatically result in the establishment of reproductive isolation. The known facts do not support this contention. Copulation in most butterflies and moths, for example, takes place during the dispersal phase of the life cycle (on flowers, etc.) and not on the host plant. If it does take place on or near the host plant, it is usually only the female that is sedentary while the male undertakes relatively extensive flights.

Ecological factors function simultaneously as isolating mechanisms only under two sets of circumstances. First if there is a difference in the breeding period. If one of two closely related species breeds only in sunlight, the other only in darkness, they will be effectively isolated, or, if one breeds only in the spring, the other only in the fall. However, there is always a twilight and a summer to connect the separated breeding periods. Furthermore, there is no evidence or probability that such drastic differences can develop within a single local population nor by single mutations (see below).

The other possibility is furnished by species in which mating always takes place on the host species and host selection is entirely rigid. Such rigid host selection has primarily a genetic basis although it may be reinforced by conditioning. Switching over to a new host would thus be tantamount to the establishment of a new species. The difficulties in this case are several. First of all, there are the heterozygotes that serve as intermediaries between the old and the new host (see below). Secondly, species that are *that* rigidly adapted to one host probably have rather low survival value on a new host, unless the new host is in a different environment. In that case, the scheme would be merely a modification of spatial speciation. However, the mechanism is possible and deserves further investigation. An evolutionary analysis of mo-

nophagous families, of insects is badly needed.

(c) *Conditioning without isolation.* Thorpe, Cushing, and other recent authors believe that conditioning could under certain circumstances play a considerable role in the origin of new species. This interest in conditioning goes back to a revival of Baldwin's theory of Organic Selection which is most fully stated in his book (1902). This theory states in short that if a population enters a new environment there will be a selective premium on mutations that would give a genetic basis to the previously non-genetic adaptive characters. This process of the substitution of modifications by mutations, which simulates direct action of the environment, has found considerable attention in Russia, as reported by Gause (1947). As a matter of fact, there is nothing strikingly new in this theory. It merely paraphrases two well-known facts, namely that adaptive characters are favored by natural selection, and that the more adaptable a species is the more easily it may enter a new environment; Both of these facts are in harmony with the concept of geographical speciation. To prove that organic selection and conditioning play an important role in speciation, it must be demonstrated that these processes reduce gene flow between the new and the parental habitat below the point where it interferes with the establishment of genetically controlled isolating mechanisms. Do the experiments on conditioning support this assumption?

An experiment by Cushing (1941) conducted in support of the hypothesis that olfactory conditioning is "one way in which an isolation may arise within insect populations" may be analyzed in more detail. A stock of the species, *Drosophila guttifera*, which normally inhabits fungus but had been kept in the laboratory on the ordinary corn-molasses-agar medium, was subdivided into two strains, one continued on this laboratory medium ("controls"), the other on a mushroom extract medium ("mushroom conditioned"). Given a

choice of a laboratory and mushroom medium for egg laying, the control flies in four sets of trials (A-D) laid 19.5 per cent eggs on the laboratory medium, while the mushroom conditioned flies laid only 8 per cent of their eggs on this medium. Does this experiment indicate that conditioning can split one population into two? I believe not. To begin with, 80.5 per cent of the eggs laid by flies conditioned and selected for many generations to lay on the laboratory medium chose the mushroom extract medium. This illustrates strikingly the powerful influence of the genetic constitution of these fungus flies. On the other hand, among the reconditioned flies 8 per cent still laid eggs on the laboratory medium. Translating this into terms of the natural environment it means that there would be a continuous very active gene flow from the population in one food niche to the population in the other. Furthermore, contrary to Cushing's opinion, selection seems to have played a role in his and other similar experiments. Even inbred laboratory strains have much concealed variability and the first generation or early generation, in such "conditioning" experiments are often characterized by high mortality. This happened also, in the experiment of Meyer and Meyer (1946) who succeeded in transferring a strain of *Chrysopa vulgaris* to a new prey (the coccid *Pseudococcus comstocki*). The success of the experiment is ascribed by the authors to natural selection by means of the survival of those larvae which were physiologically adapted to the new kind of food. There was high mortality in the first three generations. That the selection of the medium on which eggs are deposited has a genetic basis is confirmed also by the work of Masing (1946) who developed lines in a dumpy stock of *Drosophila melanogaster* in which the females preferred either a sugary or a non-sugary medium for egg deposition. The obvious correlation with the intestinal yeast flora was not examined. It may be mentioned incidentally that the attempt by Dobzhansky and Mayr

(1945) to affect the degree of sexual isolation between two species of *Drosophila* by raising the larvae jointly in the same containers was not successful. In conditioning experiments by Thorpe (1939), the possible effect of selection was carefully eliminated. *Drosophila melanogaster* flies normally have a slight avoidance of air scented with essence of peppermint oil. Given a choice of pure and scented air, only 35 per cent of the normal flies chose the scented air. During 21 experimental tests, 2 showed 50 per cent or more preference, 5 showed 40–49 per cent, 7 showed 30–39 per cent, and 7 showed only 22–29 per cent preference for the peppermint scented air. Freshly-hatched experimental flies that had been raised in a medium containing 0.5 per cent peppermint essence showed 67.0 per cent preference for scented air. This confirmed and extended the earlier work of Thorpe and Jones (1937) and of Thorpe (1938) on conditioning parasitic insects for new hosts. Significant as the work is, it does not prove that conditioning can prevent or even drastically reduce gene flow between the two kinds of environment if they are "available in mosaic distribution."

As stated in the previous section, the role of conditioning is that it assists in the invasion of new habitats by conspecific populations. However, extrinsic factors will have to inhibit gene flow to and from these new populations to permit them to develop into separate species.

The discussion of conditioning is not complete without reference to "locality conditioning." Thorpe (1945) is correct in giving much weight to the degree of sedentariness and the homing ability in the speciation process. As Rensch and others have pointed out (Magr, 1942), the less the degree of dispersal in a species—and homing as well as locality conditioning cuts down dispersal—the greater the extent of speciation and incipient speciation. It is well known that in social insects, as well as in adult birds and many other animals, there is an amazing degree

of *Ortstreue*. However, even though this phenomenon serves to lower the magnitude of the dispersal factor  $m$  (Wright, 1943), it by no means eliminates it completely. Dispersal operates in social insects through the nuptial flights, and in birds through the scattering of the juveniles. Least of all can such "locality conditioning" lead to the fission of a local population into several sympatric ones. The importance of *Ortstreue* is that it enhances the efficiency of external barriers. The role of this and other intrinsic factors is discussed in another publication (Mayr, 1948b).

(d) *Preadaptation*. Preadaptation plays an important role in several of the hypotheses associated with sympatric speciation. It is postulated that individuals actively search for the habitat for which they are preadapted. Needless to say, there is not a shred of evidence for this claim. There is a dispersal phase in the life cycle of every species during which many individuals are carried onto unsuitable locations and perish. Others may survive during favorable seasons and form the nucleus of a new population only to be wiped out again during the first adverse season. Finally, an occasional individual may have an unusually favorable gene combination which will permit some of its descendants to flourish in the new locality. This can be observed all the time along the ecological and geographical margin of the range of a species. I know of no evidence, however, that would indicate that a dispersing individual ever actively searches for a habitat for which it is "preadapted."

#### *Difficulties Created by the Hypothesis of Sympatric Speciation*

Sympatric speciation is usually postulated to explain certain ecological aspects in the speciation pattern which some authors consider inexplicable by geographic speciation. These authors overlook that sympatric speciation creates new difficulties that are avoided by the theory of geographical speciation. These difficul-

ties can essentially be classified in two groups.

(a) Neglect of dispersal. Dispersal is conspicuously neglected in all schemes of sympatric speciation, even though it is one of the basic properties of organic nature. There is a dispersal phase in the life cycle of every species. It is the adult stage in most insects with wingless larvae. In these species mating usually does not take place on the host or food plant, and hence there is no reproductive isolation between the various host races.

But, even where mating takes place on the food plant, there is a dispersal period at one stage of the life cycle. If a form, which usually lives on plant *a*, develops some individuals which colonize plant *b*, there is no reason why the offspring of the *b* individuals should not recolonize plant *a*, nor why there should not be repeated colonizations from *a* to *b*. Thus the conditions are not favorable for the establishment of a discontinuity if there is no spatial isolation between *a* and *b*. The same is true for host selection in parasites.

It is known that certain birds are extremely sedentary and live throughout the breeding season or even throughout their adult life within a restricted territory. However, even in these species, there is a certain amount of dispersal before the juvenile takes up its first territory. There seems no logical connection between the first and the second part of the statement: "Birds tend to be strongly territorial animals and the claim that geographical isolation always precedes other kinds of isolation seems premature" (Thorpe, 1945). Territoriality is a property of individuals, while speciation deals with populations.

Sessile marine organisms always seem to have a larval stage in which they may be dispersed by ocean currents for hundreds of miles and during which the populations within this area are thoroughly mixed up. This factor is often overlooked as, for example, by Test (1946) in her thesis of sympatric species

in the limpets of the genus *Acmaea*. Ecological isolation, in order to be effective, must be able to prevent the mixing of the to-be-separated populations in spite of dispersal.

There are quite a number of cases among insects where the female ordinarily does not leave the host plant or where she selects the medium for egg-laying before fertilization. Among the scoliced beetles, for example, the females bore holes under the bark. The males search them out in these tunnels and mate with them there. Here appears to be a potential mechanism for the rapid development of new monophagous races. Unfortunately, none of these cases has ever been carefully analyzed. Furthermore, even in such a scheme there are many difficulties for sympatric speciation, such as the dispersal of the males and of the young females, as well as the reversibility of all conditioning that is not genetically reinforced.

(b) Genetic *difficulties*. The most serious weakness of most schemes of sympatric speciation is that they make untenable genetic assumptions. The principal one is that mutations produce new "types" as if genetic change was an "all or nothing" mechanism. Actually new mutants in diploid bisexual animals always occur first in heterozygous condition. Such heterozygotes will form the bridge between individuals with the new character in homozygous condition and the individuals of the parental population. To escape this difficulty all sorts of auxiliary assumptions have to be made. A new isolating mechanism cannot appear as a dominant mutation *A* because the single bearer (*Aa*) of such a mutation would at once be effectively isolated from all other individuals of his species. Furthermore, there is much evidence, to be discussed below, that a single mutation will not produce such a drastic result as complete reproductive isolation without simultaneous deleterious effects on viability.

Hence, genetic models of sympatric speciation customarily operate with recessive

mutations. C. Stern (in litt.) suggested to me the following mechanism [his wording slightly modified by me] :

"Let the animal *AA*, which is host specific on plant 1, have the mutation *a* which in homozygous condition produces host specificity for plant 2. Let us then make the following assumptions :

"Assumption 1: Let *AA* live only on plant 1.

"Assumption 2: Let *aa* live only on plant 2.

"Assumption 3: Let the heterozygotes *Aa* be exactly like *AA*.

"Assumption 4: Let there be little or no dispersal in the reproductive phase so that *A* animals do not meet *aa* animals.

"Assumption 5: Let *A* be ill adapted to plant 2.

"Assumption 6: Let *aa* be ill adapted to plant 1.

"Assumption 7: Let segregated *aa* formed on plant 1 have difficulties in finding plant 2, even though the original *aa* found 2.

"Then there will be little mixing between the populations on 1 and 2 and the opportunity is provided for a gradual piling up of additional genetic differences between these populations."

In this scheme seven separate assumptions are made, of which at least four are necessary to have the scheme work. The present example involved a shift in the genetic basis for habitat preference. Schemes that work with the time element are dependent on a similar pyramiding of arbitrary assumptions. One such scheme may be formulated as follows :

"Let there be a species *AA* which breeds from April 1–15, let there be in this species a mutation *a* which in homozygous condition shifts the breeding season to the period April 25–May 10 . . . etc. etc." Some of the objections to the assumptions made in this scheme are the following :

(1) It is highly unlikely that such an important part of the life cycle of the species as the breeding time ever depends on a single gene. In fact, there will be a selective premium to have in every population a number of factors in balanced condition that affect the breeding season.

(2) If a mutation occurs in one of these loci, it may shift the onset of breeding by a few days, but it is very unlikely that such a mutation would be so drastic as

to eliminate overlapping of the breeding seasons.

(3) If there had been available a period suitable for breeding adjoining the present breeding period, it would have long since become incorporated into the breeding season in view of the normal fluctuation of the breeding season in a large population of individuals and the ever-present mutation pressure.

(4) The gene complex of an organism has been selected for thousands of generations to find optimum ecological conditions for the growth of its offspring in the period immediately following the breeding season. The offspring of individuals suddenly shifted out of their normal breeding season would be at a strong selective disadvantage.

A population can become adapted for a new breeding season only slowly by a gradual genetic reconstruction. Geographical isolation is necessary to permit this process to go on undisturbed. The shift of the breeding season is usually associated with a shift into a new breeding range where the changed season is advantageous.

The same arguments hold when a shift from diurnal to nocturnal breeding is involved or any of the other schemes that operate with time as the isolating factor.

The usual assumptions made both in the habitat preference and in the seasonal isolation schemes are

- (1) that the heterozygotes are like one of the homozygotes,
- (2) that the two phenotypes (for habitat preference or breeding season) are discontinuous, that is, that a single mutation ( $A \rightarrow a$ ) produces complete isolation, and
- (3) that—in the case of habitat selection—mating takes place in the newly-adopted habitat.

Although all three assumptions are possible, in particular 1 and 3, the relevant evidence is only rarely produced. The most vulnerable assumption is that a

harmonious, viable mutation can produce such striking effects as postulated under 2.

The whole subject is still dominated by the early De Vriesian thesis of the origin of species by single mutations. Unfortunately; no data are available on the number of gene differences between newly arisen and parental species, but some information is available on the order of magnitude involved. The weakness of such considerations is, of course, that not only the quantity but also the quality of mutations is important. A mutation on a single locus may be more important in affecting isolation between two populations than the mutations of one hundred other loci.

All individuals in sexually reproducing species (except identical twins) can be expected to be genetically different or, to put it in other words, to differ by several mutations. These are not merely minor changes, but may include a high percentage of lethals as shown by the work in *Drosophila*. There is much evidence, on the basis of morphological, physiological, immunological, and pathological studies, that two individuals of a single interbreeding human population may differ by hundreds of genes. If iso-alleles are at all common, as indicated by the work of Stern, the number of gene differences may actually be a multiple of the maximum figure now proposed.

It has not been possible in most present studies to give more than a minimum estimate of gene differences. Charles and Goodwin (1943) calculated that the morphological differences between the leaves of two hybridizing species of goldenrods (*Solidago sempervirens* and *S. rugosa*) depended on a minimum of 21 loci. The flower characters of different geographical populations of *S. sempervirens* differed by a minimum of 5-9 genes (Goodwin, 1944). Unfortunately, the method does not permit calculation of the real number of differences, which may well be 10 or more times the minimum number. Boyce (1946) showed that the often-quoted calculations are invalid which attempted to

prove that a high protein strain of corn differed in at least 20-40, but possibly 200-400 genes from the original strain. Such a tremendous genetic difference between closely related strains, if confirmed, would have been most significant. Irwin and Cumley (1947) have shown, that about one-half of the total number of chromosomes are involved in the serological differences between two species of doves of the genus *Streptopelia* (Senegal and Ring Dove). C. C. Tan (1946) showed that there are many genetic factors which control the isolating mechanism between *Drosophila pseudoobscura* and *D. persimilis*, and that they are mostly located in the X and the second chromosome. Sketchy as these data are, they indicate that even closely related species differ in a large number of genes.

The degree of morphological difference between two species is an exceedingly unreliable measure of the number of genetic differences between them. Many sibling species of *Drosophila* are virtually indistinguishable morphologically even though they may differ by scores, if not hundreds, of genes. This is indicated by their cytological, ecological, and physiological differences, as well as by their partial or complete sterility. It is for this reason also doubtful whether Shull (1945, 1946) is correct in assuming that in two species of lady beetles of the genus *Hippodamia* "no large number of mutations would be required to evolve one species from the other or both from a common stock."

If the acquisition of reproductive isolation were a matter of a single gene mutation, one would expect isolating mechanisms to be simple. However, most isolating mechanisms between closely related species that have been studied thoroughly were found to be multiple. There always seem to be involved (a) differences in the ecological requirements, (b) reduction of the mutual sexual stimulation, and (c) reduction in the number and the viability of the offspring. On close analysis even these three categories turn out to be composite. For example, the mutual

sexual stimulation may be reduced simultaneously by differences in scent, color patterns, rhythm and pattern of display movements.

There is a selective advantage in this multiplicity for two reasons. One is that there is less loss of zygotes if a species is to rely on the mutually reinforcing action of a number of different mechanisms rather than on a single one which is subject to an occasional breakdown. The other reason is that the isolating mechanisms must protect the species from interbreeding not only with one but with *all* related species. It is very unlikely that a single mechanism will furnish complete protection against all other species. Finally, there are no genetic difficulties in gradually building up a multiple isolating mechanism in spatially segregated populations.

Before closing the discussion on the possible genetic basis of sympatric speciation, a word needs to be said about "specific modifiers." As Muller (1942) has pointed out, there will be a selective advantage for genes that act to increase the adaptiveness of the expression of one allele as compared to others, if there is a discontinuity in the factor to which the gene reacts. However, since habitat preference and mate preference are not controlled by the same gene, it becomes necessary that two sets of specific modifiers develop simultaneously. The probability that this will occur unassisted by a geographical segregation of populations is obviously very small. This is one of the reasons why the evolution of mimetic polymorphism in certain species of butterflies did not lead to the origin of a considerable number of new species, even though specific modifiers were involved.

*The Hypothesis of Sympatric Speciation is Unnecessary*

The principal reason why a hypothesis of sympatric speciation is usually proposed is that certain taxonomic or ecological phenomena are believed to be incompatible with geographical speciation.

It shall be the aim of this section to show that these phenomena are by no means in conflict with geographical speciation. The objections that have been raised are based on misunderstandings.

*The species as an aggregate of ecologically different populations.* Ecological conditions vary throughout the range of all but the most narrowly distributed species. Thus every population of a species lives in a somewhat different environment and its genotype was evolved by selection for this specific local environment. What is true for local populations is even more true for subspecies. Every geographical race shows certain ecological differences from other geographical races. It was Turesson (1922) who was the first to point this out emphatically. The taxonomist who looks at these populations looks at them from his special point of view. He investigates whether such populations show morphological differences that would be of diagnostic value. If they do, he calls such populations or groups of population subspecies. The ecologist, on the other hand, looks for ecological differences between such populations (whether or not they are morphologically characterized). If he finds such differences he calls the populations ecological races or, if he is a botanist, ecotypes. In much of the current literature these two categories, the subspecies and the ecological race, are treated as two completely distinct phenomena. The truth, however, is that they are merely two facets of a single phenomenon. Gregor (1946) has recently stated correctly that if "the term 'ecotype' [is applied] to any population differentiated in respect of any characteristic attributable to the selective action of ecological factors . . . the majority of taxonomic subspecies and varieties will on experimental examination be found to bear ecotypic characteristics." I am willing to go even further than this. I am convinced that it will be a long time before even a single subspecies is found which does not bear ecotypic characteristics. Not only has every subspecies eco-

typic characteristics, but even within most subspecies are numerous ecologically different populations. Also, ecotypes do not live in an indiscriminate mixture; they are spatially segregated from each other, even though they may intergrade marginally. Ecotypes are populations or groups of populations and so are subspecies. Botanists (e.g. Gregor, 1944, 1946), on the whole, have realized this fact more clearly than have animal taxonomists.

The closest approach to geographical races in identical environment is perhaps found on some tropical islands, but even here there are stronger ecological differences than are usually recognized. The size and the elevation of the islands are different and with them temperature and precipitation. Different islands are often situated in different ocean currents, even though in close proximity. Most important of all, however, since each island has a fauna and flora which arrived fortuitously, the composition of the biota will be different on each island. In consequence, the biotic environment of a given species will be different even where the climatic environment is the same. It was Darwin (1859) who discovered this principle: "How has it happened in the several (Galapagos) islands situated within sight of each other, having the same geological nature, the same height, climate, etc., that many of the immigrants should have been differently modified, though only in a small degree. This long appeared to me a great difficulty; but it arises in chief part from the deeply-seated error of considering the physical conditions of a country as the most important for its inhabitants; whereas it cannot be disputed that the nature of the other inhabitants with which each has to compete is at least as important, and generally a far more important element of success. . . . When in former times an immigrant settled on any one or more of the islands, or when it subsequently spread from one island to another, it would undoubtedly be exposed to different conditions of life

in the different islands, for it would have to compete with different sets of organisms. . . . If then it varied, natural selection would probably favour different varieties in the different islands" (Darwin, 1859).

The converse is equally true. I do not know of a single ecological race which is not at the same time at least a microgeographic race. This means that random contact between individuals belonging to the two populations is drastically reduced by distance and barriers, and the gene flow between the two populations is reduced in a parallel manner. To repeat, all geographical races are also ecological races, and all ecological races are also geographical races.

The crucial question from the point of view of sympatric speciation, however, is not whether ecological evolutionary divergence exists within a species, but whether it may lead to the origin of discontinuities without spatial segregation. I recorded as a case of non-genetic local variants a small colony of Yellow Wagtails (*Motacilla flava*) which had become accustomed to build their nests in *Artemisia* plants rather than on the ground (Mayr, 1942). Thorpe (1945) quotes this as an incipient sympatric isolating mechanism. The fact is that such fads, either by individuals or by local populations, are quite common in animals. But there is no evidence that they are primary isolating mechanisms. They are reversible and usually disappear as quickly as they appear. Furthermore, if they last, they lead only to the establishment of new intraspecific populations, not to new species. As shown above in the section on the invasion of new habitats, no case has yet been found where a shift in habitat preference, without geographical segregation, has given rise directly to a new species. In the cases described by Mayr (1942) and Miller (1942) of habitat differences within species of birds, geographical segregation is invariably involved. All the various Song Sparrow races with different ecological require-

ments to which Thorpe refers are geographically segregated.

The ecological specialization of geographical races may be far reaching. The ornithological literature abounds with cases of ecological difference between geographical races of a single species: one in coniferous woods, the other in deciduous; one in the lowlands, the other in the high mountains; one feeding largely on ants, the other largely on beetles, etc. One of the chief diagnostic characters of the various geographic races of the Red Crossbill (*Loxia curvirostra*) is the size and the shape of the bill. Long after these various races had been described, it was found that there was a close correlation between bill structure and the principal food in a given region. The food of the Crossbill consists of the seed of conifers. "The Crossbills inhabiting isolated spruce (*Picea*) forests have weak, small bills (for instance *Loxia curvirostra himalayensis*,<sup>2</sup> *L. c. altaiensis*). On the contrary, the Crossbills inhabiting isolated pine (*Pinus*) forests have big bills (for instance, *L. c. mariae* [Crimea], *L. c. polyogyna* [Tunisia], and *L. c. balearica* [Balearic Islands])" (Kirikov, 1940). The most interesting aspect of these host-adapted races of the Crossbill is that they are geographical races. In each region a geographical race evolved which is optimally adapted for feeding on the most common conifer of the region. In the few cases where spruce and pine races of the Crossbill are now found in close proximity or even interdigitating, the evidence indicates that this is a secondary development.

The most thorough analysis of adaptive features in geographical races of birds is Lack's (1947) study of Darwin's finches (Geospizinae). Most of the geographical races are shown to differ ecologically, but no evidence is found for the sympatric evolution of these ecological races. Amadon (1947) in a similar fashion has shown the importance of geo-

graphical isolation for the development of races of Drepaniidae that are strikingly different in their ecologies.

The picture that emerges from all recent studies is that species show an amazing degree of local adaptability. Species adjust themselves to every occupied environment within the boundaries of their range. As long as these populations are in contiguous contact, there is no serious reduction of gene flow. The ecological variability within a species results in increased intraspecific variability and thus furthers evolutionary divergence. Without an extrinsic reduction of gene flow, however, the ecological variability cannot become a primary source of discontinuity.

The ecological *differences* between species. In her review of speciation among the limpets of the genus *Acmaea* Test (1946) makes the following statement: "Along the west coast of North America occur nine species of one subgenus (*Colisella*) affording every indication of close relationship; yet having either completely concurrent or encompassed ranges. In as much as the obviously parental form has the greater range in every instance in which the range of one species is encompassed by that of another . . . it becomes practically impossible to explain the situation in terms of geographical speciation." I have quoted this statement in full because it is quite typical of the reasoning of the authors who believe in sympatric speciation. What Test found for *Acmaea* is true for the species of nearly every polytypic genus. Among birds the woodwarblers (*Dendroica*), the buntings, (*Emberiza*), the white-eyes (*Zosterops*), the whistlers (*Pachycephala*), the weavers (*Ploceus*), and the hawks (*Accipiter*)—to mention only a few genera—afford good examples of closely related sympatric species. There are many even more impressive examples among insects (*Drosophila*, *Anopheles*, *Aedes*) and in other groups of invertebrates. When these groups of closely related, partially or wholly sympatric spe-

<sup>2</sup> Feeds mainly on larch (*Larix*) (Lack, 1944b).

cies are studied carefully, it is found—with rare exceptions—that each of the species has its own ecological niche. It is this observation which serves as the starting point for the hypothesis of sympatric speciation by ecological segregation. It is argued that since these species are partially sympatric their ecological differences could not have developed in geographical isolation. Lack (1944, 1947) has submitted a different interpretation. He shows conclusively that on the basis of the Gause (1934) principle no two related species can persist in the same locality without possessing ecological differences. Ecological difference between related sympatric species is thus merely proof for the efficacy of competition and natural selection but not for any particular method of speciation. There is no conflict whatsoever between the fact that related species differ ecologically and the assumption that they have originated by geographical speciation (Mayr, 1948b). It is fully consistent with the known facts to assume that the ecological differences had previously been developed in geographical segregation.

#### *Reputed Instances of Sympatric Speciation*

The most convincing proof for the importance of geographical speciation is the abundance of incipient cases. Hence, if there is an additional process of sympatric-ecological speciation, it should be possible to find for it also incipient cases. Indeed, there are numerous taxonomic and ecological situations that have been interpreted in the past as constituting such incipient cases. It will be shown in this section that the evidence in these cases is misinterpreted and that the facts are completely consistent with the theory of geographical speciation. The relevant phenomena can be organized under four headings: sibling species, lake swarms, secondary zones of intergradation, and insufficiently analyzed cases.

(1) *Sibling species*. Many of the cases of so-called "ecological or physiological"

cases of the literature are nothing but sibling or cryptic species. There is no evidence that these sibling species have evolved in any other way than by geographical speciation. This has been discussed elsewhere (Mayr, 1942, 1948a) in considerable detail and this point does not need to be taken up again.

(2) *Lake swarms*. It is well known that "species flocks" occur in all the larger and older freshwater lakes. This has been found independently by the students of fishes, crustaceans, mollusks, and other freshwater organisms. There are, for example, 178 species of Cichlid fishes in Lake Nyasa in East Africa and more than 300 species of Gammarid crustaceans in Lake Baikal. Lake Lanao on the island of Mindanao in the Philippines, the large lakes of Celebes, and other tropical and subtropical lakes in all parts of the world are also famous for their rich endemic faunas. Since it seems at first sight impossible to conceive that these sympatric faunas could have originated by geographic speciation, Woltereck, Herre, and others have postulated various processes of "explosive" speciation. None of these proposed schemes was ever worked out in detail, but they all involve either macrogenesis (the origin of new systematic categories by a single mutation step) or various forms of homogamy (assortive mating) (e.g. Kosswig). The objections to such theories have been discussed above.

The fact that the species of these swarms are now sympatric and that they live according to the Gause principle in different ecological niches in order to minimize competition has led previous authors astray. Rensch (1933) has indicated the right solution. It is that these species have come into contact only after they had evolved and after they had acquired their ecological differences. It is sometimes thought that the 58 endemic species of Cichlids in Lake Victoria (east Africa) developed since that lake originated (i.e. during the past 20,000–50,000 years). Everything 'we know about the

rate of speciation (in fishes and other animals) is opposed to this conclusion. There are now 223 species of fish known from Lake Nyasa, including 194 endemic ones. Of the 178 species of Cichlidae 174 are endemic. These are divided in many genera, of which the genus *Tilapia* is comprised of six species in Lake Nyasa, four of which are endemic (Bertram, Borley, and Trewavas, 1942). Among these six species three are quite distinct, while the other three are difficult to distinguish. One of these three species is restricted to the north end of the lake (*T. karongae*), the second one (*T. squamipinnis*) occupies a zone near the shore, while the third species (*T. lidole*) appears to inhabit a more pelagic although overlapping zone. The females of the inshore species, especially those carrying fry, enter river mouths and inlets. The interesting point here is that apparently complete facilities exist for gene flow between these species if it were not prevented by sexual isolation. The ecological specialization has not reached the point where it would prevent contact between individuals of these species in breeding condition.

"Old fresh-water lakes are, for fresh-water faunas, very much what old islands are for terrestrial faunas. They permit the survival of old elements which have long since become extinct in the surrounding areas. It seems to me that students of fresh-water faunas have vastly underestimated the age of the species with which they are working. The evidence for this is quite overwhelming for Lake Baikal, Lake Tanganyika, Nyasa, and so forth. The statement by the proponents of explosive speciation that ecological speciation precedes the establishment of discontinuity is not in the least plausible, if we remember that these habitats are in continuous contact with each other and that there is no evidence for the establishment of biological isolating mechanisms as long as unrestricted interbreeding takes place between the inhabitants of the different sympatric ecological niches. On the other hand, no objections seem to

exist against the assumption that species flocks originated by multiple colonizations, corresponding to the double and triple colonizations and the archipelago speciation among island animals" (Mayr, 1942).

None of the lake flocks has so far been analyzed from a broader point of view. Such questions need to be answered as: What species are found only in part of the lake, like *Tilapia karongae* in northern Lake Nyasa? What species have discontinuous ranges within a given lake? Are the nearest relatives of a given species found in the same lake, or in some neighboring tributary or other lake? Has the inventory of the freshwater faunas of all the present and former tributaries of these lakes been completed and how do these faunas compare with the lake fauna?

A recent analysis of the faunas of the lakes of central Asia has had the unexpected result to show that many of the famous "endemics" of Lake Baikal have, in fact, a rather wide distribution. Lake Baital is indeed a living museum preserving the remnants of several freshwater faunas that were formerly widespread in central Asia (Kozhov, 1946). The exact geological age of a given lake is rather irrelevant if it has become the receptacle of previously existing faunas. Lake Lanao in Mindanao may have originated within the late Pleistocene, but it contains an apparently Tertiary fauna which may have originated in several separate river systems. Trewavas (1947) suggests that the sudden rise or fall of water level in a lake may be a factor in speciation. This is improbable if the entire lake shore is inhabited by a continuous population living everywhere under identical conditions. Her scheme, however, works very well if, for example, a number of disconnected estuaries are involved, each with somewhat different conditions. A sudden rise of water level may wipe out all but the few most pelagic individuals in a shallow estuary, while in a deep estuary the entire population may move simply inland with the shore line. If the isolation has lasted

sufficiently long, the more pelagic population can move into the estuary of the inshore species without hybridizing. The result would be two ecologically different and partially sympatric species.

There must be situations where one might be able to study the origin of a species flock *in statu nascendi*. Hubbs and Raney (1946) have recently described such a potential case. In Lake Waccamac in North Carolina each of the genera *Notropis*, *Fundulus*, *Boleosoma*, and *Menidia* has developed an endemic form during the last quarter of the Pleistocene. These streamlined lake forms may or may not be reproductively isolated from their allopatric ancestral forms. However, if repeated invasions of the respective species complexes would occur, after reproductive isolation had been established, it would lead to the formation of species flocks. The environment in the lake is very different from the environment of the tributary streams and this undoubtedly leads to a considerable acceleration of the evolutionary rate. In this respect lakes are very much like islands, as pointed out before (Mayr, 1942). However, even though the rate of evolutionary divergence is much accelerated, there is no evidence that the origin of discontinuities differs in principle from that in terrestrial animals.

(3) *Secondary contiguity of ecologically different subspecies*. An ever increasing number of cases is being described in the literature where two ecologically very distinct subspecies are found to have adjacent or even interdigitating ranges. Such cases are often quoted as proving sympatric speciation. Actually, there is, of course, in these cases nearly always spatial segregation and, furthermore, it can often be demonstrated that the present contiguity is a rather recent phenomenon. In the mayfly *Stenonema interpunctatum* there are four intergrading subspecies with only partially separated ranges (Spieth, 1947). Most of the range of *S. i. heterotarsale* in the Lake Erie-Ontario region is overlapped by the

subspecies *canadense* and *interpunctatum*. "Obviously there must be a definite survival value attached to each of the populations or they would quickly fuse into one variable one." *S. i. interpunctatum* and *canadense* emerge earlier in the season, *heterotarsale* later. On the basis of the present distribution pattern it appears probable that the four subspecies originated during the Pleistocene in the following districts: *interpunctatum* in the Mississippi valley, *canadense* in Canada, *frontale* on the U. S. Atlantic coast, and *heterotarsale* in the Lake Erie-Ontario district. Most of the present range overlaps are due to the post-Pleistocene range expansions of *interpunctatum* and *frontale*. The most interesting aspect of this case is that during their geographical segregation each of these forms acquired a number of physiological characteristics or adaptations to special, narrow ecological niches so that now several of these "subspecies" can live in various parts of the same stream without losing their identity.

Similar cases have been described in fishes. The nominate race *nigrum* of the small fish *Boleosoma nigrum* has a very wide range in the United States. Within its range is found the subspecies *eulepis* which is more completely scaled on cheeks, nape, and breast. The nominate race occurs in lakes and streams with a firm (sandy or rocky) substratum, while *eulepis* is a fish of estuaries, rather extensive and quiet or slow-moving lowland waters, characterized by moderate or dense growths of aquatic vegetation, and on bottoms composed at least in part of mud or silt. The interesting aspect of this case is that the range of *eulepis* consists of more or less discontinuous pockets or foci of abundance, surrounded by peripheral areas of intergradation with the nominate race, but more or less restricted to the Great Lakes region. The morphological differences are not phenotypic modifications through life in the specific habitat niche, but have a genetic basis as shown by Lagler and Bailey

(1947). Physiological differences (oxygen and temperature tolerance, etc.) are presumably associated with the morphological ones, but they have not yet been investigated. There are two alternative explanations of this case. Either one presumes that in each stream and lake a quiet-water race developed in spatial segregation, or one believes that the present proximity of the races is a secondary phenomenon. Although both solutions are possible, I tend to the second one for two reasons. In many "eulepis habitats" in the range of *nigrum*, this subspecies appears to be absent, particularly in that part of the range of *nigrum* that is outside the Great Lakes region. The second reason is the comparative homogeneity of eulepis in its now disjunct range. The available evidence suggests that eulepis once had a continuous range (? during one of the later stages of the Pleistocene) but that the somewhat superior *nigrum* invaded its range and forced it to retreat into the quiet water pockets where eulepis is superior. It would be very interesting to know more about the genetic mechanisms that prevent the breaking up of the *nigrum*- and eulepis-gene complexes that are superior in their respective habitats. That such mechanisms seem to exist is indicated by the work of Heuts (1947) on the races of the Stickleback (*Gasterosteus aculeatus*) in western Europe. In this case again two rather distinct races or race-complexes seem to have come into secondary contact without losing their identity.

In polymorphic populations there is also sometimes evidence that each of the various types has originated in a definite locality. Much of the evidence concerning mimetic polymorphism in butterflies points that way and Southern (in *litt.*) suggests that such spatial segregation may have been involved in the development of host races in cuckoos. During periods of range expansions, it can sometimes even be demonstrated that some "ecologically variable" species consist actually of various ecotypes, each of

which has a different geographical origin (Peitzmeier, 1942).

This evidence can be summarized in the statement that it appears that ecologically contrasting subspecies normally originate in spatial segregation and usually even in complete geographical isolation. Contact zones between such subspecies are usually zones of secondary intergradation (Mayr, 1942).

(4) *Insufficient* evidence. Sympatric speciation is often postulated in cases in which the available evidence is insufficient to draw any conclusions. Vaghin (1946), for example, uses it to account for the presence of two forms of the oligochaet *Chaetogaster limnaei* in mollusks, one a commensal in the mantle, the other an endoparasite in the kidney. No evidence is given on the question whether or not the two populations are reproductively isolated. They might be two good (sibling) species which have invaded the host at different times, but they might also be members of a single population which acquire different characteristics depending on the organ of the mollusk which they invade. This case is merely quoted as a single example of numerous similar ones that one finds continuously in the literature. They are without value for the problem of sympatric speciation unless the analysis is carried a good deal further.

#### THE FACTORS OF SPECIATION

A balanced evaluation of the respective roles in speciation of ecological and geographical factors is still missing. Both work closely together and "there is no geographic speciation that is not at the same time ecological and genetic speciation" (Mayr, 1942). The first step in the speciation process is the founding of a new intraspecific population. This is very often possible only through a shift in ecological tolerance, and insofar Thorpe's statement is quite correct that an ecological rather than a geographical event may be the first step in speciation, or—since the new population will be not only ecologically different but also spatially

segregated from the parental one—that the ecological event (adaptation to a new ecological niche) is at least simultaneous with the first geographical event. This first step leads to the establishment of a spatially segregated population that is exposed to different selection pressure owing to the more or less differing ecological conditions under which it lives. The ecological factors here lead to evolutionary divergence. These populations will drift apart genetically (probably at an accelerating rate!) until a discontinuity through reproductive isolation develops, provided extrinsic barriers reduce dispersal (= gene flow.) to such an extent that it can no longer neutralize the effects of the different selection pressures in the two populations. It is still unknown whether this can happen between contiguous populations without the help of extrinsic factors that reduce gene flow.

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#### SUMMARY

All degrees of geographical isolation are known, resulting in a complete interruption or only slight reduction of gene flow between the isolated populations. The term microgeographical isolation may be used where only short distances are involved.

The establishment of a new intraspecific population is usually associated with a shift in the ecological characteristics of such a population. All subspecies show ecological differences, and no "ecological races" are known that are not also at least "microgeographical."

It is unproven and unlikely that reproductive isolation can develop between contiguous populations.

Many of the assumptions made in the various hypotheses of sympatric speciation

are erroneous. The evidence usually cited as proving sympatric speciation is fully consistent with the theory of geographic speciation. The concept of sympatric speciation creates many difficulties avoided by the concept of geographic speciation.

Sympatric speciation, if it occurs at all, must be an exceptional process. The normal process of speciation in obligatorily sexual and cross fertilizing organisms is that of geographical speciation.

#### LITERATURE CITED

- ALPATOV, B. W. 1925. Über die homogame und pangame Paarung im Tierreiche. *Zool. Anz.*, **62**: 329–331.
- AMADON, D. 1947. Ecology and the evolution of some Hawaiian birds. *Evolution* **1**: 63–68.
- ARMSTRONG, T. 1946. Differences in the life history of the codling moth, *Carpocapsa pomonella* (L.), attacking pear and apple. *Canadian Entomologist*, **77**: 231–233.
- BALDWIN, J. M. 1902. Development and evolution. Macmillan and Company, 395 pp.
- BERTRAM, C. K. R., J. J. H. BORLEY, AND E. TREWAVAS. 1942. Report on the fish and fisheries of Lake Nyasa. Crown Agents of the Colonies, 181 pp.
- BLAIR, W. F. 1947. Estimated frequencies of the buff and gray genes (G, g) in adjacent populations of deer mice (*Peromyscus maniculatus blandus*) living on soils of different colors. *Contr. Lab. Vert. Biol.*, **36**: 1–16.
- BOYCE, A. M. 1935. The codling moth in Persian Walnuts. *Jour. Econ. Ent.*, **28**: 864–873.
- BOYCE, S. W. 1946. Estimation of genes in inheritance of quantitative characters. *Nature*, **157**: 657.
- CATCHPOOL, E. 1884. An unnoticed factor in evolution. *Nature*, **31**: 4.
- CHARLES, D. R., AND R. H. GOODWIN. 1943. An estimate of the minimum number of genes differentiating two species of goldenrod with respect to their morphological characters. *Amer. Nat.*, **77**: 53–69.
- CROZIER, W. 1918. Assortative mating in a nudibranch, *Chromodoris zebra*. *Jour. Exp. Zool.*, **27**: 247–292.
- CUSHING, J. E. 1941. An experiment on olfactory conditioning in *Drosophila guttifera*. *Proc. Nat. Acad. Sci.*, **27**: 496–499.
- DAHL, E. 1889. Die Bedeutung der geschlechtlichen Zuchtwahl bei der Trennung der Arten. *Zool. Anz.*, **12**: 262–266.
- DARWIN, C. 1859. On the origin of species by means of natural selection, or the preservation of favored races in the struggle for life. John Murray, London.

- DIEDERICH, G. W. 1941. Non-random mating between yellow-white and wild types of *Drosophila melanogaster*. *Genetics*, 26: 148.
- DOBZHANSKY, TH., AND E. MAYR. 1945. Experiments on sexual isolation in *Drosophila*. IV. Modification of the degree of isolation between *Drosophila pseudoobscura* and *Drosophila persimilis* and of sexual preferences in *Drosophila prosaltans*. *Proc. Nat. Acad. Sci.*, 31: 75-82.
- GAUSE, G. F. 1934. *Struggle for existence*. Williams and Wilkins Company, 160 pp.
- . 1947. *Problems of evolution*. *Trans. Conn. Acad. Arts and Sciences*, 37: 17-68.
- GERSHENSON, S. 1941. Additional data concerning the mating system in wild populations of common hamster (*Cricetus cricetus*). *Compt. Rend. Acad. Sci. URSS*, 31: 155-156.
- GOODWIN, R. H. 1944. The inheritance of flowering time in a short-day species, *Solidago sempervirens* L. *Genetics*, 29: 503-519.
- GREGOR, J. W. 1944. The ecotype. *Biol. Reviews*, 19: 20-30.
- . 1946. Ecotypic differentiation. *New Phytologist*, 45: 254-270.
- HEUTS, M. J. 1947. Experimental studies on adaptive evolution in *Gasterosteus aculeatus* L. *Evolution* 1: 89-102.
- HOBGEN, L. 1946. *An introduction to mathematical genetics*. W. W. Norton and Co., Inc., 260 pp.
- HUBBS, C. L., AND E. C. RANEY. 1946. Endemic fish fauna of Lake Waccamac, North Carolina. *Misc. Publ. Mus. Zool., Univ. Mich.*, No. 54, 30 pp.
- IRWIN, M. R., AND R. W. CUMLEY. 1947. A second analysis of antigenic differences between species in 'Columbidae'. *Genetics*, 32: 178-184.
- KIRIKOV, S. V. 1940. On the connection between the Red Crossbills and the coniferous trees. *Bull. Acad. Sci. URSS (Biol.)*, 359-376.
- KOSSWIG, C. 1947. Selective mating as a factor for speciation in Cichlid fish of East African lakes. *Nature*, 159: 604.
- KOZHOV, M. 1946. Baikalian mollusks from Lake Kossogol (Mongolia). *Compt. Rend. (Doklady) Acad. Sci. URSS*, 52: 365-368.
- LACK, D. 1944a. Ecological aspects of species formation in passerine birds. *Ibis*, 86: 260-286.
- . 1944b. Correlation between beak and food in the Crossbill, *Loxia curvirostra* Linnaeus. *Ibis*, 86: 552-553.
- . 1947. *Darwin's finches*. Cambridge University Press, 208 pp.
- . 1948. The significance of ecological isolation. [Princeton Symposium.] [In press.]
- LAGLER, K. F., AND R. M. BAILEY. 1947. The genetic fixity of differential characters in subspecies of the percid fish, *Boleosoma nigrum*. *Copeia*, 50-59.
- MANNING, T. H. 1942. Blue and lesser snow geese on Southampton and Baffin Islands. *Auk*, 59: 158-175.
- MASING, R. A. 1946. Experiments on selection for selective egg-deposition in *Drosophila melanogaster*. *Comptes Rend. Acad. Sci. URSS*, 51: 393-396.
- MAYR, E. 1942. *Systematics and the origin of species*. Columbia University Press, 334 pp.
- . 1948a. The bearing of the new systematics on genetical problems. *Advances in Genetics*, 2 (in press).
- . 1948b. Speciation and systematics. *Princeton Symposium* (in press).
- MEYER, N. F., AND Z. A. MEYER. 1946. The formation of biological forms in *Chrysopa vulgaris* Schr. (Neuroptera, Chrysopidae). *Zool. Jour.*, 25: 115-120.
- MILLER, A. H. 1942. Habitat selection among higher vertebrates and its relation to intra-specific variation. *Amer. Nat.*, 76: 25-35.
- MULLER, H. J. 1942. Isolating mechanisms, evolution and temperature. *Biological Symposia*, 6: 71-125.
- PEARSON, K. 1900. *The grammar of science*. Second ed., Adam and Charles Black, London, 548 pp.
- PEITZMEIER, J. 1942. Die Bedeutung der oekologischen Beharrungstendenz für faunistische Untersuchungen. *Jour. f. Ornith.*, 90: 311-322.
- RENSCH, B. 1933. Zoologische Systematik und Artbildungsproblem. *Verh. Deutsch Zool. Ges.*, 19-83.
- ROMANES, G. J. 1897. *Darwin and after Darwin*. Vol. III, Open Court Publishing Co., 181 pp.
- SHULL, A. F. 1945. Inheritance in lady beetles. III. Crosses between variants of *Hippodamia quinquesignata* and between this species and *H. convergens*. *Jour. Hered.*, 36: 149-160.
- . 1946. The form of the chitinous male genitalia in crosses of the species *Hippodamia quinquesignata* and *H. convergens*. *Genetics*, 31: 291-303.
- SPETT, G. 1929. Zur Frage der Homogamie und Pangamie bei Tieren, Untersuchungen an einigen Coleopteren. *Biol. Centralbl.*, 49: 385-392.
- . 1931. Gibt es eine partielle sexuelle Isolation unter den Mutationen und der Grundform von *Drosophila melanogaster* Meig.? *Zeitschr. ind. Abst. Vererb.*, 60: 63-83.
- SPIETH, H. T. 1947. Taxonomic studies on the Ephemeroptera. IV. The genus *Stenonema*. *Ann. Ent. Soc. Amer.*, 40: 87-122.

- STRESEMANN, E. 1942. Oekologische Sippen-, Rassen-, und Artunterschiede bei Vögeln. Jour. für Ornith., **91**: 305-328.
- TAN, C. C. 1946. Genetics of sexual isolation between *Drosophila pseudoobscura* and *D. persimilis*. Genetics, **31**: 558-573.
- TEST, A. R. 1946. Speciation in limpets of the genus *Acmaea*. Contr. Lab. Vert. Biol., **31**: 1-24.
- THORPE, W. H. 1938. Further experiments on olfactory conditioning in a parasitic insect. The nature of the 'conditioning process. Proc. Royal Soc., **126**: 370-397.
- . 1939. Further studies on pre-imaginal olfactory conditioning in insects. Proc. Royal Soc., **127**: 424-433.
- . 1945. The evolutionary significance of habitat selection. Jour. Animal Ecol., **14**: 67-70.
- AND F. G. W. JONES. 1937. Olfactory conditioning in a parasitic insect and its relation to the problem of host selection. Proc. Royal Soc., **124**: 56-81.
- TIMOFEEFF-RESSOVSKY, N. W. 1943. [Erbliche und 'oekologische Isolation.] Jour. für Ornith., **91**: 326-327.
- TREWAVAS, E. 1947. Speciation in Cichlid fishes of East African lakes. Nature, **160**: 96-97.
- TURESSON, G. 1922. The species and the variety as ecological units. Hereditas, **3**: 100-113, 210-350.
- VAGHIN, V. L. 1946. On the biological species of *Chaetogaster limmaei* K. Baer. Compt. Rend. Acad. Sci. URSS, **51**: 481-484.
- VALENTINE, J. M. 1943. Insect taxonomy and principles of speciation. Jour. Washington Acad. Sci., **33**: 353-358.
- . 1945. Speciation and raiation in *Pseudanophthalmus* (Cave beetles). Trans: Conn. Acad. Arts and Sci., **36**: 631-659.
- WAGNER, M. 1889. Die Entstehung der Arten durch raumliche Sonderung. Benno Schwabe, Basel.
- WRIGHT, S. 1943. Isolation by distance. Genetics, **28**: 114-138.

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#### BOOKS ON EVOLUTION RECEIVED

- BABCOCK, ERNEST BROWN. 1947. The genus *Crepis*. Part I. The taxonomy, phylogeny, distribution, and evolution of *Crepis*. Univ. Calif. Publ. in Bot., vol. 21, 197 pp. Part II. Systematic treatment, vol. 22, pp. 199-1030.
- HEBERER, GERHARD. 1943. Die Evolution der Organismen. Jena, Gustav Fischer, 774 pp. Contains the following contributions: Dingler, Hugo. Die philosophische Begründung der Deszendenztheorie, pp. 2-19.—Zimmermann, Walter. Die Methoden der Phylogenetik, pp. 20-56.—Rensch, Bernhard. Die biologischen Beweismittel der Abstammungslehre, pp. 57-85.—Ziendorf, Werner. Idealistische Morphologie und Phylogenetik, pp. 86-104.—Lorenz, Konrad. Psychologie und Stammesgeschichte, pp. 105-127.—Weigelt, Johannes. Palaontologie als stammesgeschichtliche Urkundenforschung, pp. 131-182.—Rüger, Ludwig. Die absolute Chronologie der geologischen Geschichte als zeitlicher Rahmen der Phylogenie, pp. 183-218.—Franz, Viktor. Die Geschichte der Tiere, pp. 219-296.—Magdefrau, Karl. Die Geschichte der Pflanzen, pp. 297-332.—Bauer, Hans, and N. W. Timoféeff-Ressovsky. Genetik und Evolutionsforschung bei Tieren, pp. 335-429.—Schwanitz, Franz. Genetik und Evolutionsforschung bei Pflanzen.—Ludwig, Wilhelm. Die Selektionstheorie, pp. 479-520.—Herr, Wolf. Domestikation und Stammesgeschichte, pp. 521-544.—Heberer, Gerhard. Das Typenproblem in der Stammesgeschichte, pp. 545-585.—Krogh, Christian. Die Stellung des Menschen im Rahmen der Säugetiere, pp. 589-614.—Gieseler, Wilhelm. Die Fossilgeschichte des Menschen, pp. 615-682.—Reche, Otto. Die Genetik der Rassenbildung beim Menschen, pp. 683-706.—Weinert, Hans. Die geistigen Grundlagen der Menschwerdung, pp. 707-734.
- HUTCHINSON, J. B., R. A. SILOW, AND S. G. STEPHENS. 1947. The evolution of *Gossypium* and the differentiation of the cultivated cottons. Oxford University Press, 160 pp.
- LACK, DAVID. 1947. Darwin's finches. Cambridge University Press, 208 pp.